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Please direct correspondence to:

Kenneth A. Hashagen, Jr., Editor
California Fish and Game
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SYSTEMATICS OF GOLDEN TROUT, *SALMO AGUABONITA,* FROM THE SIERRA NEVADA [1]

J. R. GOLD
Genetics Section
Texas A & M University
College Station, TX 77843
and
G. A. E. GALL
Department of Animal Science
University of California
Davis, CA 95616

We examined the meristics, morphology, and dentition of 504 specimens from 14 trout populations in the Little Kern River basin area of the Sierra Nevada, California. This region is thought to circumscribe the range of the golden trout subspecies *Salmo aguabonita whitei.* On the basis of mean similarities, Euclidian distances, and projections from canonical analysis, the 14 populations were separated into two distinct phenetic groups: one represented by a sample from the headwaters of Deadman Creek (DMC), and the other by the remaining samples. Little Kern River samples were compared with those from the upper Kern River and upper South Fork Kern River (SFKR) known to represent the golden trout subspecies *Salmo aguabonita aguabonita,* and with two samples of domesticated strains of rainbow trout, *Salmo gairdneri.* The number of trout populations surveyed from the Little Kern basin through 1974 totals 15 and includes samples from headwaters and other portions of most of the permanently flowing streams north of Soda Spring Creek. Data reported in different studies are in agreement and may be summarized as follows: (i) two isolated headwater trout populations, one from DMC and the other from upper Soda Spring Creek (USSC), are virtually the same, but differ markedly from other upper Little Kern trout; (ii) distinguishing features of DMC-USSC trout include low number of vertebrae and pyloric caecae, and high number of lateral series scale rows; (iii) phenetically, DMC-USSC trout are nearly identical to *S. a. aguabonita;* and (iv) in multivariate orientation, most upper Little Kern trout occupy positions between DMC-USSC trout and *S. gairdneri.* These patterns of geographic variation among Little Kern trouts are not easily explained by models based on chance, adaptive, or non-genetic effects. We suggest that the DMC-USSC trout are most closely related evolutionarily or phyletically to *S. a. aguabonita* and are descended from among the first trouts to enter Kern basin waters either before or during the last glacial retreat. Other present-day upper Little Kern trout populations, and several named forms from the Little Kern and elsewhere in the upper Kern basin, may reflect varying degrees of introgression from past hybridizations of native goldens with introduced non-native trout such as *S. gairdneri.* They may also be derivatives of a redband-like trout which later entered the upper Kern basin, or, alternatively, they may be natural derivatives of the original endemic golden trout. The DMC-USSC trout are best referred to *S. aguabonita,* a species which at present includes trout from DMC, USSC, SFKR, GTC (Golden Trout Creek), and perhaps a few other streams in the upper Kern River basin.

INTRODUCTION

The systematics and taxonomy of the trouts native to the Kern River basin in the Sierra Nevada, California, are not well understood. At least four golden trout-like forms, initially recognized as full species, and one subspecies of rainbow trout have been described from the region, although the taxonomic validity

[1] Accepted for publication November 1980.

of some of these forms has been the subject of considerable debate. At present, the general consensus is that only one golden trout species, *Salmo aguabonita* Jordan, and possibly one subspecies of rainbow trout, *Salmo gairdneri gilberti* Jordan, are endemic to Kern basin waters. An excellent historical critique of the early literature on Kern basin trouts may be found in Schreck and Behnke (1971).

For primarily historic and distributional reasons, *S. aguabonita* is considered to comprise two subspecies. One of these, *S. a. aguabonita,* is restricted to the northeastern part of the upper Kern River basin, and includes populations [2] from Golden Trout Creek and the South Fork Kern River (Gold and Gall 1975*a*). The other subspecies, referred to as either *S. a. whitei* or *S. a. gilberti,* includes trouts from the upper Little Kern River basin (Shapovalov, Dill, and Cordone 1959, Schreck 1969, Schreck and Behnke 1971, Legendre, Schreck, and Behnke 1972, Gold and Gall 1975*a, b*). Recognizable morphological differences between these two geographically disjunct subspecies are few. Populations of *S. a. aguabonita* usually are distinguished from those of *S. a. whitei* by less intense spotting and greater brilliance in colors (Evermann 1906).

The status of the Kern River rainbow, *S. g. gilberti,* is questionable. Schreck (1969) and Schreck and Behnke (1971) synonomized *S. g. gilberti* with *S. aguabonita* from the Little Kern basin (formerly *S.* (*a.*) *whitei* Evermann) on the basis of similarities in the ranges and means of a few meristic characters (principally lateral series scale rows) between trout collected from the Kern and Little Kern Rivers in 1893 and 1904 and limited samples collected in 1967–1968. Since *gilberti* had priority over *whitei* in the literature, they suggested that the Little Kern golden trout be referred to as *S. a. gilberti.* They further noted that there was no geologic evidence that trout from the Kern River and the Little Kern River were ever physically isolated from each other. However, a thorough survey by Evans, Smith, and Bell (1973) revealed the existence of several natural barriers both near the confluence of the Little Kern and Kern rivers and throughout the Little Kern River basin.

The central problem confounding evolutionary relationships among upper Kern basin trout is that many present-day stream populations are of mixed or unknown ancestry. During the late 1800's and early 1900's biologists and the first Kern plateau settlers indiscriminately introduced several non-native trouts throughout the basin and transplanted many native stocks from their streams of origin to other nearby waters. Although many introductions and transplants were recorded (Evermann 1906, Ellis and Bryant 1920, Meyer 1965, Schreck 1969), it is certain that many were not. Further, several recorded 'stockings' involved trout of unknown provenance. It is important to note that a few introductions and transplants occurred before and during the time of the original descriptions of Kern basin trout.

A second source of confoundment, primarily involving Little Kern trout, is the hybridization which may have occurred between endemic goldens and rainbows introduced for recreational purposes. Between 1930–1941, almost 100,000 rainbow fingerlings were planted annually in waters throughout the Little Kern basin (Dill 1941, 1945, 1950), and stocking records list a few earlier rainbow

[2] The term population is used throughout to represent a localized random mating population. Fish taken from a restricted sampling area are assumed to represent such a population (McGlade and MacCrimmon 1979).

introductions. The degree of golden x rainbow hybridization in the Little Kern basin has not been critically assessed, but the considerable phenotypic heterogeneity observed among Little Kern trouts generally has been taken as evidence that both hybridization and backcrossing were extensive (Dill 1945, 1950, Needham and Gard 1959, Schreck 1969, Schreck and Behnke 1971, Gold and Gall 1975*a*, Christenson 1978). Certainly, the laboratory successes of hybridization among these and other western trouts (Hartman 1956, Gould 1966, Dangel 1973, Gold, Pipkin, and Gall 1976, 1979) suggest that reproductive isolating mechanisms are far from complete.

A final problem is the lability in external meristic morphology which characterizes most salmonid fishes. Much of this variation is presumably a response to differing environmental conditions during early stages of development. Several examples among salmonids in nature are cited in Mayr (1973:p. 145), and examples from laboratory experiments are abundant (Tåning 1952, Garside 1966, Kwain 1975). Salmonids, particularly western trouts, also are noted for numerous instances of convergent or parallel evolution (Behnke 1970, 1972), which further tends to obscure actual evolutionary relationships.

Previously (Gold and Gall 1975*a, b, c,* Gold 1975, Gall *et al.* 1976), we reported the occurrence of at least two significantly distinct phenetic groups of golden-like trout in Little Kern waters. One group, represented by samples from upper Soda Spring Creek (USSC) and Deadman Creek (DMC), had close phenetic and genetic affinities to geographically disjunct *S. a. aguabonita.* A second group, represented by samples from lower Soda Spring Creek (LSSC) and the Little Kern River (LKR) near Peck's Canyon Creek, was roughly intermediate in morphology, karyology, and biochemical-genetic profile between *S. a. aguabonita* and *S. gairdneri.* We suggested that the DMC-USSC trout were pure populations of an endemic Little Kern golden trout; whereas the LSSC-LKR trout probably represented remnants of golden x rainbow hybridization. In this paper, we continue our survey of geographic variation among present-day Little Kern trouts. Included are morphological analyses of samples from 14 populations (504 individuals), an assessment of the variation among present-day trout from the upper portion of the Little Kern basin, and a consideration of this variation in regard to systematics and classification of Kern basin trout.

MATERIALS AND METHODS

Thirteen samples of trout from the Little Kern River and one sample from the headwaters of the South Fork of the Kaweah River were collected between 19 August and 23 September 1974. Approximate collection localities and positions of barriers to upstream migration are provided (Figure 1), as well as geographic information and keys to sample sites (Appendix Table 1). Two Little Kern localities (DMC and LSSC) previously sampled (Gold and Gall 1975*a, b*) were included to allow comparisons between years as well as among all populations examined through 1974. The South Fork Kaweah sample was included since Evermann (1906) described *Salmo whitei* from there, where it had been introduced from Soda Spring Creek. Other trout populations examined for comparative purposes included one sample of *S. a. aguabonita* from the South Fork Kern River (provided by E. P. Pister, Fishery Biologist, Calif. Dept. Fish and Game), and two samples of domesticated rainbow trout (provided by Mt. Shasta State Hatchery personnel). Specimens were returned to the laboratory, sacrificed,

tagged for identification, preserved in ethanol, and deposited in reference collections at the Department of Wildlife and Fisheries Science, Texas A&M University.

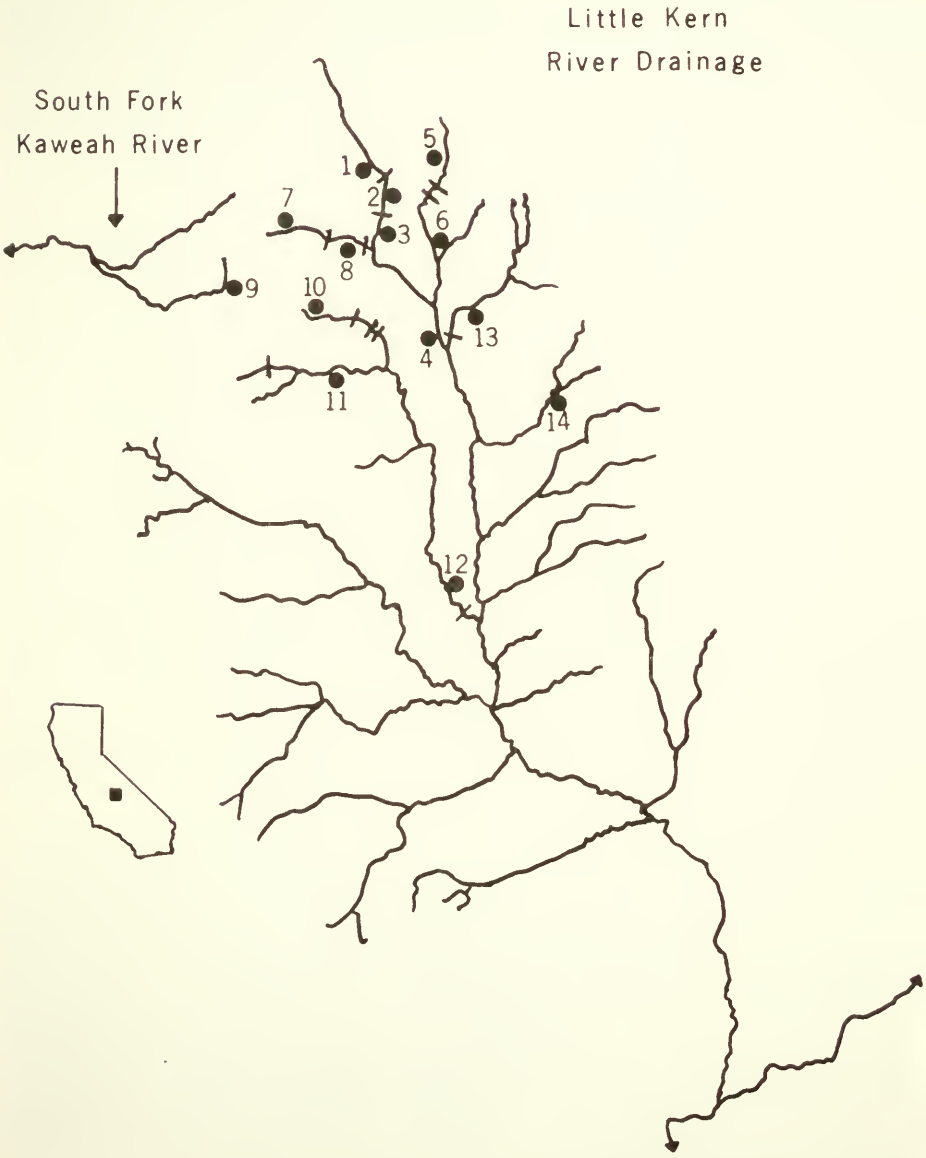

FIGURE 1. A map of the Little Kern River drainage showing the locations of fourteen 1974 collection sites, and the locations of natural barriers to upstream migration. Collection sites are as follows: 1-LKR-1; 2-LKR-2; 3-LKR-3; 4-LKR-4; 5-USGC; 6-LSGC; 7-UWMC; 8-LWMC; 9-GM; 10-DMC; 11-MSSC; 12-LSSC; 13-RC; and 14-TMC (cf. text for further details).

Measurements and meristic data were taken from the left side following methods described in Gold and Gall (1975*a*). Branchiostegal rays were counted on both left and right sides. Interneurals (dorsal fin pterygiophores), interhaemals (anal fin pterygiophores), and epurals were enumerated from radiographs. Basibranchial and other dentition were examined using a technique suggested by R. J. Behnke (outlined in Gold 1977:p. 1860). All specimens were examined in a random sequence and identified only by tag number. Observed means, standard deviations, and ranges for 13 meristic characters and fork length for each of the 14 samples are provided (Appendix Tables 2*a–b*). Values for males and females are combined since tests of sex and sex x location interaction effects for each character were non-significant.

All data were initially subjected to univariate statistical analyses using the mean, variance, and Fisher's third and fourth moment statistics. Of 14 characters, only distributions for parr marks and epural number appeared non-normal. Homogeneity of means for all characters was tested using two-way (sex by locality) analysis of variance. Sex and sex x locality interaction effects were non-significant ($P > 0.05$); however, significant heterogeneity ($P < 0.01$) among means due to locality was detected for all characters except epural number. Mean separation tests involving only the 12 normally distributed characters were accomplished using Duncan's multiple range analysis weighing the least significant ranges for unequal sample sizes (Sokal and Rohlf 1969).

Multivariate statistical analyses using only the 11 normally distributed meristic characters were employed to project phenetic affinities and relationships among samples. Specific procedures included UPGMA cluster analysis of a Euclidian distance matrix, multivariate analysis of variance (MANOVA), and canonical analysis. Each multivariate procedure was carried out using computer programs in SAS, the Statistical Analysis Series designed and implemented by Barr *et al.* (1976). Four different criteria (Hotelling-Lawley's Trace, Pilla's Trace, Wilks's Criterion, and Roy's Maximum Root Criterion) were used to test the hypothesis of no overall locality effect in the MANOVA. All four tests produced significant F values ($P < 0.01$), indicating significant morphological heterogeneity among samples due to locality.

Canonical analysis of the data provided weighted combinations of characters which maximized the distinction among samples. Characteristic roots and orthogonal vectors were extracted from the variance-covariance matrix, and means for each sample or locality were computed along each vector. Each successive orthogonal axis, termed a canonical variate, extracted the next best combination of characters to discriminate among samples. Each eigenvalue and its corresponding canonical variate (characteristic root) represented an identifiable fraction of the total variation. The relative importance of each original character to a particular canonical variate was computed by multiplying the vector variable coefficient by the grand mean of the dependent variable (individual character), summing all variable values for a particular vector, and then computing the percent of relative importance of each character per vector.

RESULTS

Results of mean separation tests involving the 11 normally distributed meristic characters and fork length are shown in Tables 1*a* and *b*, in addition to estimates of grand means and error mean squares from analysis of variance. Since age data

were not recorded, the observed differences in mean fork length could stem from several factors, including heterogeneous age distributions within and among populations. Comparisons among samples with significantly different means generally revealed no consistent associations between mean value of any single meristic character and geographic location. No clinal trends with latitude or with altitude were apparent, and geographically contiguous samples (e.g., UWMC-LWMC, USGC-LSGC, etc.) were not necessarily more similar than geographically discontinuous ones. Exceptions to the latter were the LKR-2, 3, and 4 samples which were very similar if not identical for means of all characters.

TABLE 1a. Observed Means, Grand Means, and Error Mean Squares (from Analysis of Variance *) of Six Characters for Fourteen Samples of Trout from the Little Kern River Basin Area.

Sample	*Fork length*	*Pyloric caecae*	*Dorsal rays*	*Anal rays*	*Pectoral rays*	*Pelvic rays*
LKR-1	15.0^{a}	35.86^{b}	12.57^{cde}	11.14^{cd}	14.76^{a}	9.78^{de}
LKR-2	14.1^{bcde}	36.78^{bc}	12.78^{a}	11.08^{bc}	15.30^{cd}	9.78^{de}
LKR-3	13.6^{abcd}	37.39^{bcde}	12.58^{cde}	10.94^{abc}	15.61^{def}	9.79^{e}
LKR-4	13.3^{abc}	39.32^{de}	12.29^{abc}	11.10^{bcd}	15.59^{def}	9.63^{bcde}
USGC	14.6^{de}	36.79^{bcd}	12.32^{abcd}	11.00^{bc}	15.41^{cde}	9.47^{bc}
LSGC	14.0^{bcd}	38.55^{bcde}	12.35^{abcd}	11.06^{bc}	15.61^{def}	9.71^{cde}
RC	14.7^{de}	37.29^{bcde}	12.69^{de}	11.37^{d}	15.09^{abc}	9.77^{de}
UWMC	14.6^{de}	36.16^{b}	12.29^{abc}	10.97^{bc}	14.79^{a}	9.39^{b}
LWMC	13.3^{abc}	38.83^{cde}	12.46^{bcde}	11.34^{d}	15.69^{ef}	9.54^{bcde}
DMC	12.5^{a}	33.24^{a}	12.15^{ab}	10.68^{a}	15.68^{ef}	9.00^{a}
MSSC	13.0^{ab}	35.97^{b}	12.05^{a}	10.90^{abc}	15.33^{cd}	9.51^{bcd}
LSSC	14.5^{cde}	37.52^{bcde}	12.06^{a}	11.10^{bcd}	15.16^{bc}	9.71^{cde}
TMC	14.1^{bcde}	39.68^{e}	12.15^{ab}	11.03^{bc}	15.80^{f}	9.60^{bcde}
GM	14.8^{de}	43.67^{f}	12.11^{ab}	10.83^{ab}	14.97^{ab}	9.67^{cde}
$\bar{X}$	14.0	37.66	12.35	11.04	15.34	9.60
EMS	...	23.48	0.46	0.26	0.43	0.25

* Means with identical superscripts are not different at $P \leq 0.05$.

The striking feature revealed by the mean separation tests was the marked distinctness of the DMC sample. For 7 of the 11 meristic characters, DMC fish possessed either the lowest or highest observed mean value; for the remaining 4, DMC means were not significantly different from the observed low (or high) sample mean. This distinctness was especially apparent in number of pyloric caecae, pelvic fin rays, vertebrae, and lateral series scale rows, where DMC fish were essentially unique among the 14 samples.

Comparisons of the number of shared means (Table 2) provided a qualitative measure of morphological similarities among samples. DMC was easily the most dissimilar, sharing an average of only 3.0 means in common with all other samples. LWMC and GM were the next most dissimilar, sharing an average of 5.85 means with other samples. The remaining 11 samples from the Little Kern River appeared to form a relatively close, cohesive grouping, having among them over 8 of 11 means in common. Three sets of pairwise comparisons (LKR-2 and LKR-3; LKR-3 and LKR-4; and TMC and LSGC) were statistically identical for means of all 11 characters.

TABLE 1*b*. Observed Means, Grand Means, and Error Mean Squares (from Analysis of Variance *) of Six Characters for Fourteen Samples of Trout from the Little Kern River Basin Area.

Sample	*Branchiostegal rays (total)*	*Vertebrae*	*Gill rakers (l)*	*Scales in lateral series*	*Interneurals*	*Interhaemals*
LKR-1	23.22^{bcd}	61.62^{g}	20.49^{cdef}	155.5^{g}	14.51^{bcd}	12.30^{bcde}
LKR-2	23.18^{bc}	61.50^{efg}	20.53^{def}	162.4^{bcd}	14.78^{de}	12.15^{bcd}
LKR-3	22.79^{b}	61.55^{fg}	20.58^{def}	164.5^{bcde}	14.73^{cde}	12.24^{bcde}
LKR-4	23.32^{bcde}	61.10^{cdef}	20.27^{bcde}	161.4^{bc}	14.49^{bcd}	12.12^{bcd}
USGC	23.29^{bcde}	60.41^{ab}	20.71^{ef}	160.5^{b}	14.32^{bc}	12.00^{abc}
LSGC	23.00^{bc}	61.03^{cde}	20.97^{f}	165.2^{cde}	14.81^{de}	12.32^{cde}
RC	22.86^{b}	60.80^{bc}	19.86^{ab}	165.4^{cde}	15.06^{e}	12.54^{ef}
UWMC	22.97^{bc}	60.97^{cd}	19.50^{a}	166.3^{de}	14.29^{bc}	12.16^{bcd}
LWMC	23.83^{de}	61.31^{defg}	19.91^{abc}	174.1^{f}	14.63^{cd}	12.83^{f}
DMC	23.91^{e}	60.06^{a}	19.97^{abcd}	183.5^{g}	13.82^{a}	11.71^{a}
MSSC	22.97^{bc}	61.05^{cde}	20.31^{bcde}	175.8^{f}	14.33^{bc}	11.95^{ab}
LSSC	22.13^{a}	61.26^{cdefg}	20.13^{bcde}	161.2^{bc}	14.13^{ab}	12.45^{de}
TMC	23.08^{bc}	61.18^{cdefg}	20.38^{bcdef}	166.7^{e}	14.45^{bcd}	12.15^{bcd}
GM	23.56^{cde}	61.42^{defg}	19.94^{abcd}	166.2^{de}	13.81^{a}	11.75^{a}
$\bar{X}$	23.16	61.10	20.25	166.3	14.44	12.18
EMS	1.43	0.82	1.29	69.9	0.63	0.44

* Means with identical superscripts are not different at $P \leq 0.05$.

In order to quantitatively assess phenetic similarities among the 14 samples, Euclidian distances between sample pairs were computed from a standardized data matrix, basically following the methodology of Gold and Gall (1975*a*:p. 256). The resulting distance matrix (Table 2) was then clustered using UPGMA average linkage analysis to produce a non-overlapping, hierarchical phenogram (Figure 2). The cophenetic correlation coefficient (matrix with phenogram) was 0.911.

The phenetic affinities among samples depicted in the phenogram essentially paralleled similarities revealed by the comparisons of the number of shared means. DMC was the last group to cluster, being well separated in average distance (21.79 units) from the rest. The fact that DMC has closest affinity to MSSC (13.55 units, Table 2) was not reflected in the phenogram, and may be attributed in part to the distortion at lower clustering levels which usually accompanies cluster analyses (Sneath and Sokal 1973). The similarity between DMC and MSSC stemmed primarily from the high number of lateral series scale rows in these two samples as compared to considerably lower numbers in other samples (Table 1*b*). However, MSSC was closer in average distance (11.65 units) to all other samples than to DMC.

The other 13 samples were closer to one another in average Euclidian distance than any was to DMC. GM, LWMC, MSSC, and LKR-1 were the most divergent, joining the group individually at successively higher clustering levels (14.19, 13.39, 12.51, and 11.37 units, respectively). Individual characters affecting the distinctness of these four samples were high number of pyloric caecae (GM), high number of vertebrae and low number of lateral series scale rows (LKR-1), and high number of lateral series scale rows (MSSC and LWMC). The remaining

nine samples divided into two groups, one containing UWMC and LSSC (9.43 units), and the other LKR-2, 3, 4, TMC, LSGC, USGC, and RC (10.46 units). Separation between these two groups could not be attributed to any single character or suite of characters and appeared to result from small differences in several characters. No further inferences regarding phenetic affinities were made since higher level clusters were apparently affected by sampling variation. This was indicated by the fact that LKR-3 and LKR-4 did not join until 7.08 units, yet the two samples were statistically identical for means of all 11 characters (Table 2).

Canonical analysis of the 11 character data set yielded 11 characteristic roots (canonical variates) which accounted for all of the phenetic variation. Of these, only the first explained an appreciable proportion (48.3%) of the variation and had an eigenvalue greater than 1.0. Characteristic root II accounted for 14.1% of the variation, but its eigenvalue of 0.327 was not significantly different from zero (Wilks's lambda test). Uni-dimensional Hubbs-o-grams displaying univariate statistics of each sample along canonical variate I are provided (Figure 3). Characters contributing heavily to separation along this vector included number of vertebrae, lateral series scale rows, pelvic fin rays, and pectoral fin rays (Table 3).

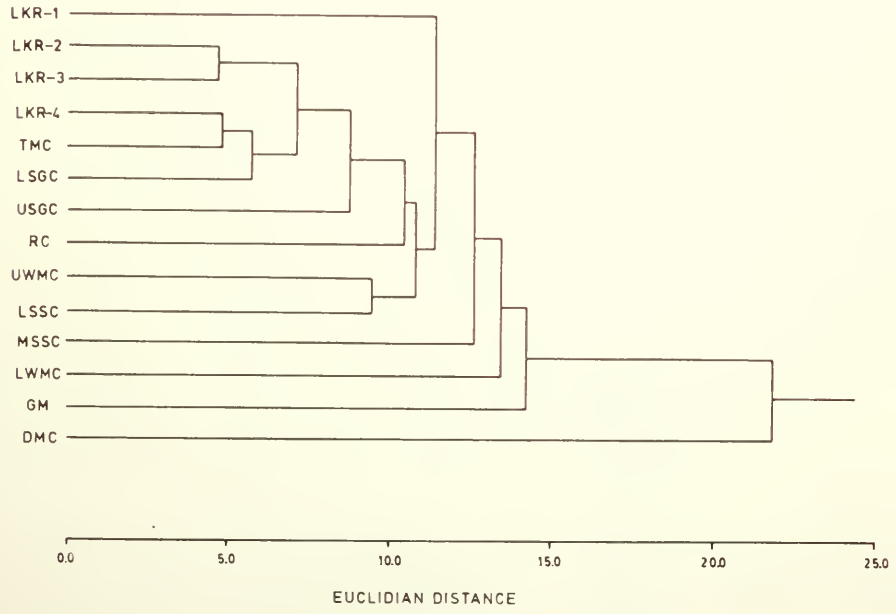

FIGURE 2. Phenogram from UPGMA cluster analysis of the Euclidian distance matrix. The cophenetic correlation r_{cs} was 0.911.

TABLE 2. Matrices of Mean Similarity * (lower left) and Euclidian Distances (upper right) Between Pairs of Fourteen Samples of Trout from the Little Kern River Basin Area.

Sample	*LKR-1*	*LKR-2*	*LKR-3*	*LKR-4*	*USGC*	*LSGC*	*RC*	*UWMC*	*LWMC*	*DMC*	*MSSC*	*LSSC*	*TMC*	*GM*
LKR-1	—	7.77	10.88	10.61	12.48	12.33	11.67	11.96	17.96	28.13	17.48	10.21	14.39	15.87
LKR-2	9	—	4.63	7.02	10.31	7.08	8.61	11.33	13.27	24.06	13.24	10.50	9.51	14.62
LKR-3	9	11	—	6.66	10.58	5.23	10.10	12.17	12.40	23.06	11.74	9.59	6.96	14.51
LKR-4	7	9	11	—	6.10	5.85	10.19	10.40	12.19	21.80	11.92	8.70	4.90	11.84
USGC	7	7	9	10	—	8.13	12.32	10.88	15.53	20.48	12.78	10.74	8.46	12.92
LSGC	8	10	10	10	8	—	9.59	12.58	11.48	22.00	11.25	10.08	5.61	14.60
RC	7	7	7	7	5	8	—	10.74	11.66	24.26	14.21	11.20	11.94	17.31
UWMC	7	5	7	7	7	7	6	—	14.30	18.91	9.98	9.43	11.69	12.43
LWMC	7	5	6	9	6	6	6	5	—	20.24	12.59	15.33	10.57	17.13
DMC	1	1	3	4	5	2	1	2	4	—	13.55	24.36	19.78	22.61
MSSC	7	8	7	9	9	7	6	8	5	4	—	13.01	9.54	13.77
LSSC	7	8	7	9	8	7	8	6	5	3	8	—	9.85	13.51
TMC	7	7	10	10	7	11	6	8	7	3	8	8	—	11.72
GM	5	6	5	6	5	6	4	7	5	6	7	7	7	—

* Values in each pairwise comparison refer to the number of characters with similar means.

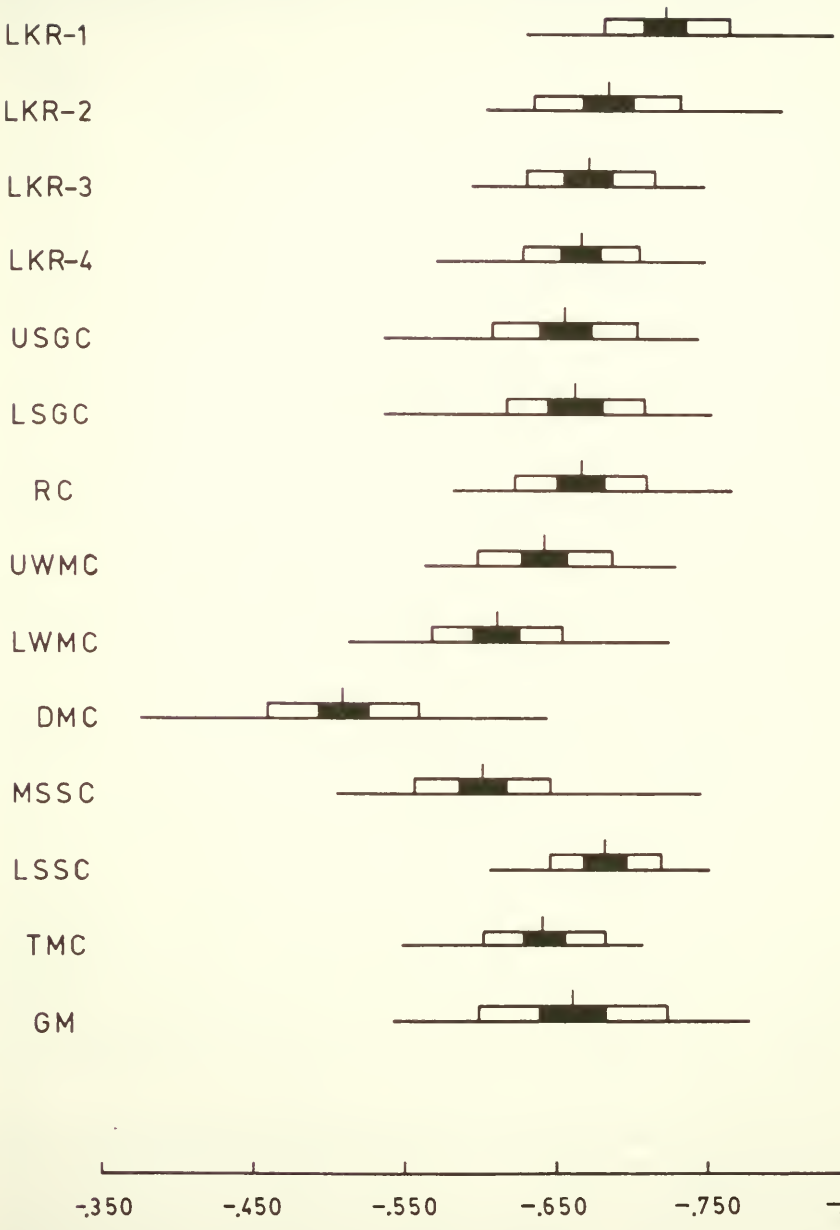

FIGURE 3. Hubbs-o-grams illustrating the phenetic positions of fourteen trout samples along canonical vector I. For each sample, the mean is indicated by the short black vertical line. Two standard errors on either side of the mean are shown by the solid black bar, and one standard deviation on either side of the mean by the white bar plus the black bar. The range is indicated by the solid black horizontal line.

TABLE 3. Variable Coefficients for Canonical Variate I with an Estimate of the Percent Influence of each Variable on the Vector for Fourteen Samples of Trout from the Little Kern River Basin Area.

Character	*Variable coefficient*	*Percent influence*
Pyloric caecae	−0.00154	1.97
Dorsal rays	−0.00161	0.68
Anal rays	−0.00573	2.15
Pectoral rays	0.02236	11.63
Pelvic rays	−0.03645	11.86
Branchiostegal rays	0.00557	4.38
Vertebrae	−0.01600	33.16
Gill rakers (I)	−0.00884	6.07
Scales, lateral series	0.00407	22.99
Interneurals	−0.00842	4.13
Interhaemals	−0.00239	0.99

The relative positions of each sample along vector I closely agree with affinities indicated by the mean similarity and Euclidian distance comparisons. DMC was well separated in 11 character space, and appeared to comprise a single, distinct phenetic group. MSSC and LWMC occupied positions somewhat less than halfway between DMC and a broad group containing the remaining 11 samples. Within the latter, most samples were phenetically similar except for LKR-1 and LSSC, which were displaced slightly to the right of the main group, and UWMC which was displaced slightly to the left (towards DMC). The affinity between UWMC and LSSC, and the distinctness of GM, suggested by the distance phenogram, were not corroborated by canonical analysis. The sample means for these groupings of the two characters (vertebrae and lateral series scale rows) which most heavily influenced vector I were: DMC (60.06, 183.5); LWMC plus MSSC (61.17, 175.0); GM (61.42, 166.2); LKR-1 plus LSSC (61.46, 158.1); and the rest (61.08, 164.0). Separation from left to right along vector I followed a trend of increasing vertebrae number and decreasing lateral series scale row number.

The foregoing indicates the presence of at least two phenetically distinct forms of trout among the 14 samples. One distinct type, represented by DMC fish, is characterized principally by low number of vertebrae and high number of lateral series scale rows. The other 13 samples form a generally homogeneous grouping, although small differences in several characters are often evident. "Marginal" samples (e.g., LKR-1, MSSC, LWMC) show divergences in apparently key characters such as lateral series scale rows, but are more similar to the main group than to DMC.

To examine these differences in relation to other trout forms, MANOVA and canonical analysis were carried out on a new data set which included samples from two populations of domesticated rainbow trout and two populations of *S. a. aguabonita* from the northeastern part of the upper Kern basin. The two rainbow trout samples were designated RTS (Shasta strain) and RTV (Virginia strain), and the two *S. a. aguabonita* samples as SFKR (South Fork Kern River) and GTC (Golden Trout Creek). Observed means, standard deviations, and ranges for several meristic characters in RTS, RTV, and SFKR are shown in Appendix Table 3. Meristic data for GTC may be found in Gold and Gall (1975*a*: p. 253). The meristic data set included only 7 of the 11 characters used earlier

since counts of interneurals, interhaemals, branchiostegal rays, and gill rakers were not available for all samples. The loss of information, however, should be minimal as these four characters usually are not discriminating among these trout (Table 3, Schreck and Behnke 1971, Gold and Gall 1975*a*).

The hypothesis of no overall locality effect in the MANOVA among the 18 samples was rejected ($P < 0.01$) by four different criteria (cf. METHODS). Canonical analysis yielded seven characteristic roots, the first of which explained 78.8% of the variation and had an eigenvalue of 4.725. Characteristic root II accounted for only 7.9% of the variation, and its eigenvalue of 0.476 was not significantly different from zero (Wilks's lambda test). Hubbs-o-grams displaying the positions of each sample along canonical variate I are shown in Figure 4, and character contributions to the vector appear in Table 4. Again, vertebrae and lateral series scale rows most heavily influenced separation, but in this analysis vertebrae number appeared to exert a relatively greater effect.

TABLE 4. Variable Coefficients for Canonical Variate I with an Estimate of the Percent Influence of Each Variable on the Vector for Eighteen Samples of Trout.

Character	*Variable coefficient*	*Percent influence*
Pyloric caecae	0.00519	8.78
Dorsal rays	0.00832	4.45
Anal rays	−0.00392	1.88
Pectoral rays	−0.01599	10.57
Pelvic rays	0.01641	6.84
Vertebrae	0.01679	44.64
Scales, lateral series	−0.00318	22.84

The relative positions of the Little Kern samples and GM were only slightly changed in this analysis. DMC remained clearly distinct from the others, and the latter were more or less phenetically the same. MSSC was still positioned approximately halfway between DMC and the main group, but LWMC appeared to be slightly displaced to the right (away from DMC). GM was definitely displaced to the right. These differences are attributable to the greater effect in this analysis of vertebrae number on separation along vector I.

Of the four comparison populations, the two rainbow samples (RTS and RTV) were well displaced to the right and markedly distinct from all other samples. The short distance between RTS and RTV is explained by the increased number of lateral series scale rows in RTS (cf. Appendix Table 3). The two *S. a. aguabonita* samples also differed slightly from one another. GTC was virtually identical to DMC in both multivariate mean (0.552 *vs.* 0.553) and variance (0.0015 *vs* 0.0017); whereas SFKR occupied a position roughly halfway between MSSC and DMC-GTC. Again, the gradient (left to right) along the vector appeared to reflect increasing vertebral number and decreasing lateral series scale row number. Considered together, all samples of Little Kern trout, GM, and the two representatives of *S. a. aguabonita* were more similar to one another than any were to the rainbow trout. A few samples (e.g., LKR-1 and GM) which were displaced to the right appeared more "rainbow-like", but the clearly distinct samples (DMC, GTC, SFKR, and perhaps MSSC) were divergent in a direction

away from rainbow trout. The similarity between DMC and GTC substantiates our earlier findings (Gold and Gall 1975*a, b*) that DMC trout are much more closely related phenetically to *S. a. aguabonita* than to trout from nearby locations in the Little Kern basin.

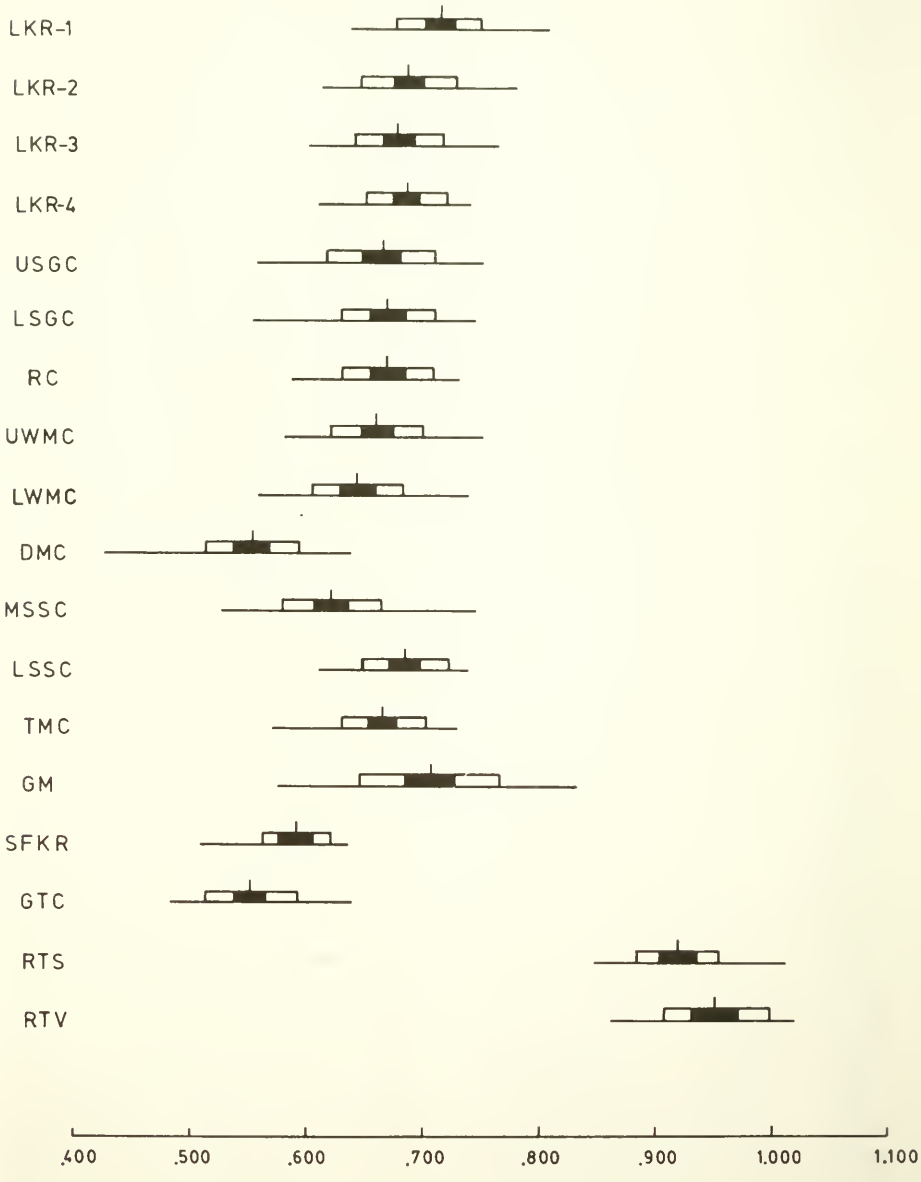

FIGURE 4. Hubbs-o-grams illustrating the phenetic positions of eighteen trout samples along canonical vector I. For further details, see Figure 3.

The last morphological examination performed on the 14 samples was a careful search for the presence of basibranchial or other unusual dentition. Of the 504 specimens examined, 88 (17.5%) possessed at least one basibranchial tooth, and a few specimens had as many as five (Table 5). In only a few instances were these teeth prominent and well developed. All samples except DMC contained individuals with basibranchial dentition, the numbers per sample ranging from 2 of 36 (5.5%) in GM to 12 of 34 (35.3%) in USGC (Table 5). The SFKR fish also were examined for dentition, but only one individual with one poorly developed basibranchial tooth was found.

TABLE 5. Distribution of Basibranchial Teeth Among Individuals in Fourteen Samples of Trout from the Little Kern River Basin Area. Numbers in Parentheses Refer to Sample Sizes.

Sample	*Number of individuals w/basibranchial dentition*	*Number of basibranchial teeth*				
		1	*2*	*3*	*4*	*5*
LKR-1 (37)	7	6	1	—	—	—
LKR-2 (40)	4	2	—	2	—	—
LKR-3 (33)	7	6	1	—	—	—
LKR-4 (41)	6	5	—	1	—	—
USGC (34)	12	7	2	2	1	—
LSGC (31)	4	2	—	—	1	1
RC (35)	10	7	2	—	—	1
UWMC (38)	9	4	2	2	—	1
LWMC (35)	9	8	1	—	—	—
DMC (34)	0	—	—	—	—	—
MSSC (39)	4	4	—	—	—	—
LSSC (31)	5	3	1	—	1	—
TMC (40)	9	7	1	1	—	—
GM (36)	2	2	—	—	—	—

The unusual "glossohyal" dentition described previously from a few specimens of *S. a. gilberti* (Schreck and Behnke 1971) and the unnamed redband trout (Schreck and Behnke 1971, Gold 1977) were found on only 13 of the 504 specimens examined. Twelve individuals possessed only one of these teeth, and one (from LWMC) had two. Samples with this type of dentition included: LSGC (4), RC (4), LKR-4 (3), LWMC (1), and LKR-1 (1).

DISCUSSION

The number of trout populations surveyed from the Little Kern basin through 1974 totals 15, and includes samples from headwaters and other portions of most of the permanently flowing streams north of the mouth of Soda Spring Creek. Morphological data reported in different studies (Gold and Gall 1975*a, b,* Gold 1975, this paper) are essentially in agreement and may be summarized as follows: (i) two isolated headwater populations, one from DMC and the other from USSC, are virtually the same in meristic morphology, but differ markedly from trout in all other upper Little Kern streams sampled; (ii) distinguishing features of DMC-USSC trout include low number of vertebrae and pyloric caecae, and high number of lateral series scale rows; (iii) phenetically, DMC-USSC trout are nearly identical to *S. a. aguabonita,* as represented by samples from GTC and SFKR; (iv) most other upper Little Kern trout are morphologically similar, but a few (e.g., MSSC, LWMC) are generally intermediate between

DMC-USSC and the rest; (v) all upper Little Kern trouts, upper South Fork Kaweah trout (GM), and *S. a. aguabonita* are more similar to one another than any are to rainbow trout (as represented by RTS and RTV in this study, and four other rainbow samples in Gold 1975); and (vi) in multivariate orientation, most upper Little Kern trout occupy positions between DMC-USSC and rainbow trout. Repeat samples from 1973–1975 (Table 6) suggest these differences are relatively stable and do not stem from sampling error. Patterns of karyotypic and biochemical-genetic variation also have been studied in a few of these populations (Gold and Gall 1975*c*, Gall *et al.* 1976), and are congruent with the morphological data.

TABLE 6. Selected Meristic Data (mean ± one standard error) from Repeat Samplings of Kern Basin Trout. Numbers in Parentheses Refer to Year Collected.

Sample	*N*	*Pyloric caecae*	*Pectoral fin rays*	*Pelvic fin rays*	*Vertebrae*	*Scales, lateral series*
DMC (73) [1]	20	30.6±0.4	15.4±0.1	9.6±0.1	59.9±0.1	181.0±1.2
DMC (74) [4]	34	33.2±0.6	15.7±0.1	9.0±0.1	60.1±0.1	183.5±1.2
DMC (75) [3]	26	35.0±0.7	15.5±0.1	10.0±0.1	60.4±0.1	178.9±1.8
USSC (73) [2]	93	32.2±0.4	15.5±0.1	9.5±0.1	60.8±0.1	181.8±0.9
USSC-1 (75) [3]	25	34.3±0.7	15.8±0.1	9.9±0.1	60.7±0.2	173.0±2.0
USSC-2 (75) [3]	24	39.8±0.9	15.2±0.1	9.6±0.1	60.6±0.2	176.4±2.0
SFKR (73) [2]	40	31.1±0.7	14.7±0.1	9.2±0.1	60.0±0.2	180.2±2.0
SFKR (74) [4]	19	31.5±0.8	14.5±0.1	9.0±0.0	59.8±0.2	172.7±1.8
LSSC (73) [2]	36	34.6±0.7	14.9±0.1	9.4±0.1	61.3±0.2	157.7±1.9
LSSC (74) [4]	31	37.5±0.8	15.2±0.1	9.7±0.1	61.3±0.2	161.2±1.4
LKR (73) [2]	56	36.0±0.7	15.0±0.1	9.8±0.1	61.4±0.2	156.8±1.5
LKR-3 (74) [4]	33	37.4±1.0	15.6±0.1	9.8±0.1	61.5±0.2	164.5±1.5
LKR-4 (74) [4]	41	39.3±0.8	15.6±0.1	9.6±0.1	61.1±0.1	161.4±1.3

Data are from [1]Gold and Gall (1975*b*); [2]Gold and Gall (1975*a*); [3]Smith (1980); and [4]this paper. LKR samples represent different localities not separated by physical barriers.

The observed patterns of geographic variation among Little Kern trouts are not easily explained by models based only on chance or adaptive effects. Under a chance model, divergence should be random in direction and inversely proportional to effective population size in magnitude. Both DMC and USSC are isolated headwater populations, and both apparently have limited population levels and low fecundity (Smith 1977). However, similar conditions prevail in many upper Little Kern streams, and thus far none of the other isolated headwater populations (LKR-1, USGC, UWMC, and TMC) have been anywhere near as divergent as DMC-USSC. It also would be difficult under a chance model to explain why the overall change in direction and magnitude in the geographically separate DMC and USSC populations is nearly the same, and why these differences appear stable from year to year. If both populations are or have been subjected to unusually severe stochastic effects, then at least some degree of divergence between the two might be expected.

Under an adaptive model, the observed patterns of variation would best be explained by assuming past or present directional selective pressures which affected only trout in DMC and USSC. However, there are no obvious ecological or habitat differences which distinguish DMC and USSC from other upper Little Kern streams (Evans, Smith, and Bell 1973; Smith 1977), and we have found no evidence of clinal variation in any meristic character. Further, if selection alone

has produced the constellation of characteristics which typify DMC-USSC trout, then similar selective pressures also must exist in GTC and SFKR. Certainly, it would be difficult to argue that habitat conditions and selective pressures in DMC and USSC are more similar to those in the distant drainages of Golden Trout Creek and the South Fork Kern River than to those in the same basin.

A third possibility is that the variation stems from differential "non-genetic" or environmental effects that radically alter embryonic developmental rate and duration (Hubbs 1922, 1926; Hamor and Garside 1976). Laboratory experiments on several fishes, including salmonids, have shown that segment numbers for most meristic characters generally increase under growth retarding conditions, and decrease under accelerating conditions (Gabriel 1944, Tåning 1952, Garside 1966, Kwain 1975). The extent of these effects in natural trout populations, however, is apparently fairly small (Behnke 1979). Schreck and Behnke (unpub. data, see 1971: p. 990) compared morphologies of introduced populations with their parental stocks in four different trout taxa (including *S. aguabonita*) and found that no more than 2% of the differences in mean values for most meristic characters (up to 5% in scale rows) could be attributed to nongenetic effects. Since the percent differences among upper Little Kern trout meristic means are considerably greater than 2% (15% in scale rows), the observed variation would appear to be the result of true genetic differentiation. There also was no indication of a parallel response in the direction of character divergence (e.g., the gradient along vector I in canonical analysis), which further argues against an environmental effects model.

The foregoing considerations suggest that the patterns of morphological and genetic variation among present-day Little Kern trouts cannot logically be accounted for by those evolutionary forces which normally promote differentiation among natural populations. The DMC and USSC trout apparently represent a unique form in the upper Little Kern basin; but given the geographic separation and absence of gene flow between the two populations, it is difficult to explain how trout in both have diverged in the same direction and to nearly the same extent. The key to the problem, however, may not lie in the dissimilarities among Little Kern trouts, but rather in the similarities between DMC-USSC trout and *S. a. aguabonita*. In almost every criterion thus far examined, including meristic morphology, karyotype, and biochemical-genetic profile, DMC-USSC trout have been more similar to *S. a. aguabonita* than to trout only a few miles distant in the same basin (Gold and Gall 1975*a, b, c,* unpubl. data, Gall *et al.* 1976). The only noticeable differences we have found, aside from geographic separation, are slight variations in number and location of body spots. DMC-USSC trout are similar, on the average, to the color plate of *S. whitei* shown in Evermann (1906), and tend to have more body spots, particularly below the lateral line. However, there is considerable variation in spotting among DMC-USSC trout, and individuals with patterns typical of present-day *S. a. aguabonita* are not infrequent (Gold and Gall unpubl. data, Smith 1977: Figures 1–3). Further, DMC-USSC trout are actually more similar in spotting to *S. a. aguabonita* than to certain Little Kern populations (e.g., LSSC) where individuals often display the profuse spotting typical of *S. gairdneri*. In short, the present evidence strongly suggests that DMC-USSC trout are little more than isolated populations of a form now considered to represent *S. a. aguabonita*.

If our interpretations are correct, and DMC-USSC trout are the same as *S. a.*

aguabonita, then their presence in the Little Kern basin may be explained under one of two hypotheses: either (i) DMC-USSC trout are relicts of a trout form which once occupied much of the upper Kern basin, and is now represented only by stocks in DMC, USSC, GTC, SFKR, and perhaps a few other streams; or (ii) they are vestiges of earlier transplants of *S. a. aguabonita* into the Little Kern basin. Unfortunately, the present data cannot distinguish between these two alternatives since both predict morphological and genetic similarity between DMC-USSC trout and *S. a. aguabonita.* However, stocking records compiled by Schreck (1969) do not list any official introductions of *S. a. aguabonita* into the Little Kern basin, and given the remoteness and terrain surrounding the DMC and USSC headwater sites it is unlikely that any introductions ever were made. On this basis we favor the first hypothesis, but note that the second cannot presently (if ever) be falsified.

What about the trout elsewhere in the upper Little Kern basin? The morphological and genetic intermediateness of most of these populations between *S. a. aguabonita* (including DMC and USSC trout) and *S. gairdneri* suggests a hybrid origin, or at least introgression (Anderson 1949) of rainbow genes into native golden populations. Stocking records (Schreck 1969) show that almost every Little Kern site thus far examined, excepting DMC, USSC, and UWMC, either received or was accessible to hatchery or other rainbow trout planted in the basin. The UWMC site, however, received a transplant of trout in 1892 from somewhere in the Little Kern River (Ellis and Bryant 1920), and also happens to be located in a small meadow adjacent to a major trail, an ideal spot for packers to have planted non-native trout.

Several aspects of the data support an introgression hypothesis. First, most upper Little Kern populations are not strictly intermediate in morphology between the two presumed parental types, but are more similar to DMC-USSC trout. This would be expected if not all planted fish crossed with natives, or if backcrossing to golden trout took place in the 30 years since the last official rainbow introductions. Secondly, trout from tributaries entering the Little Kern River below Soda Spring Creek (e.g., Alpine Creek or Mountaineer Creek), where extremely heavy rainbow introductions are known to have occurred, are morphologically more similar to *S. gairdneri* than to *S. aguabonita* (Smith 1981). Finally, the karyotypic and biochemical-genetic data suggest a small, but detectable rainbow influence (Gold and Gall 1975*c*, Gall *et al.* 1976).

As pointed out by Miller (1972) 'critical' evidence of hybrid fertility often is lacking in western *Salmo*, and it is important to note that much of the evidence for introgression in the Little Kern basin is circumstantial. Schreck (1969) and Schreck and Behnke (1971) faced the same problem in their studies of Little Kern trouts, and could only tentatively identify hybrid populations by greater meristic variability and heavier spotting patterns. In a few populations we have examined (e.g., LSSC and LKR from Gold and Gall 1975*a*) there are fish with the profuse spotting typical of *S. gairdneri.* But in others (e.g., RC) most individuals resemble Evermann's *S. whitei.* Since the genetic basis of spotting in western *Salmo* is virtually unknown, identification of 'purity' based solely on this characteristic seems a dubious prospect. There also were no apparent differences in meristic variability (Table 7) among the 14 populations (including DMC) examined in the present study. This does not falsify an introgression hypothesis, but rather demonstrates the difficulty of the problem. One might expect, for exam-

ple, that after 30 years populations would have achieved morphological stability, particularly if the amount of introgression were small.

TABLE 7. Mean Coefficients of Variance (after Soulé 1972) for Eleven Normally Distributed Meristic Characters of Fourteen Samples of Trout from the Little Kern Basin Area.

Sample	*Mean C.V. ± S.E.*
LKR-1	5.25 ± 0.80
LKR-2	5.83 ± 0.78
LKR-3	5.85 ± 0.96
LKR-4	5.65 ± 0.82
USGC	6.11 ± 0.98
LSGC	5.28 ± 0.77
RC	5.48 ± 0.88
UWMC	5.27 ± 0.62
LWMC	4.93 ± 0.71
DMC	4.79 ± 0.71
MSSC	5.06 ± 0.96
LSSC	5.36 ± 0.77
TMC	5.27 ± 0.73
GM	6.07 ± 1.02

Regardless, what is important is that the DMC-USSC trout are different from most other upper Little Kern basin trout. For key meristic characters such as vertebrae, lateral series scale rows, and pyloric caecae, the magnitude of difference invariably exceeds three standard errors of a mean, well beyond the usual limits of statistical confidence. The lone exception are MSSC trout which are divergent from the main group and toward DMC-USSC. This can easily be explained since the MSSC site is directly below both DMC and USSC and must receive occasional migrants of DMC-USSC genotype.

The above discussions have bearing on the systematics and present classifications of Kern basin trout. Briefly, five forms of trout, including four golden species and one rainbow subspecies, have been described from the Kern River drainage. The golden trouts include *S. aguabonita* Jordan (Jordan and Henshaw 1878: listed as *S. pleuriticus* Cope, Jordan 1892, 1893) from the South Fork Kern River; *S. roosevelti* Evermann (1906) from Golden Trout Creek (formerly Volcano Creek); *S. rosei* Jordan and McGregor (1924) from Culver Lake; and *S. whitei* Evermann (1906) from the Little Kern basin. Ironically, Evermann's description of *S. whitei* was based on specimens from the headwaters of the South Fork Kaweah River (Green Meadows site, this paper) where trout had been transplanted from Soda Spring Creek. The rainbow subspecies, *S. gairdneri gilberti* Jordan (Jordan and Henshaw 1878: listed as *S. irideus* and *S. tsuppitch,* Jordan 1894), was described from specimens taken in the Kern River.

Based on studies by Curtis (1934, 1935), *S. aguabonita* and *S. roosevelti* were eventually synonomized, and have gradually become classified as *S. aguabonita aguabonita* (Shapovalov, Dill, and Cordone 1959). Dill and Shapovalov (1954) synonomized *S. rosei* with *S. g. gilberti* because of earlier transplants from Big Arroyo (Creek) to Culver Lake; but Schreck and Behnke (1971) felt that *rosei* might have been a hybrid between *gilberti* and *S. a. aguabonita.* In either case, *S. rosei* is no longer considered a valid taxon. Dill (1945) was the first to refer to *S. whitei* as *S. a. whitei,* a suggestion which later became generally accepted (Shapovalov, Dill, and Cordone 1959). Schreck and Behnke (1971) synonomized *S. a. whitei* and *S. g. gilberti,* and based on karyotypic and meristic

similarities to *S. a. aguabonita* and the priority of *gilberti* over *whitei* in the literature reclassified Little Kern trout as *S. a. gilberti.* They also concurred with the synonomy of *S. aguabonita* and *S. roosevelti,* and the invalidity of *S. rosei.*

Taxonomic data for key meristic characters of pertinent upper Kern trouts and other western *Salmo* are shown in Table 8. Other comparative data for these trouts include dentary characteristics, karyotypes, and spotting patterns. The type specimens of *S. "rosei"* and *S. "whitei",* and present-day specimens of *S. a. aguabonita,* DMC-USSC trout, and *S. gairdneri* apparently do not possess basibranchial dentition; whereas individuals from the remaining groups often have one or a few of these teeth (Schreck and Behnke 1971, Schreck pers. commun., Gold and Gall 1975*a,* Gold 1977, this paper). Diploid karyotypes of *S. a. aguabonita,* DMC-USSC trout, samples from LSSC and LKR, and the redband trout contain 58 chromosomes and 104 chromosome arms (Miller 1972, Wilmot 1974, Gold and Gall 1975*c,* Gold 1977, unpubl. data). North American *S. gairdneri* also possess 104 (diploid) chromosome arms, but chromosome numbers range at least from 58–60 (Thorgaard 1976, 1977, unpubl. data). Spotting patterns on DMC-USSC trout are similar to Evermann's *"whitei"* (see also Smith 1977: Figures 1–3), but the variation in this character render it a poor taxonomic criterion. Most other trout listed in Table 8 (except *S. a. aguabonita* and *S. gairdneri*) have been described as similar in spotting to Evermann's *"whitei"* (Schreck 1969, Schreck and Behnke 1971, Gold and Gall 1975*a,* Gold 1977).

Consideration of these data lead to the following general conclusions. First, the use of *S. a. whitei* for the DMC-USSC trout (e.g., Gold and Gall 1975*a*) may no longer be appropriate. These fish are nearly the same as *S. a. aguabonita,* and may be distinguished from other upper Kern basin trout, including *S. "whitei"* or *S. a. gilberti,* by fewer pyloric caecae and vertebrae, and greater number of lateral series scale rows. On the basis of morphological and meristic criteria, the DMC-USSC trout and *S. a. aguabonita* in our opinion do not warrant formal taxonomic separation.

Secondly, most upper Little Kern trout (including GM) and the types of *S. "rosei", S. "whitei",* and *S. g. gilberti* are not separable from one another. All are more or less intermediate in morphology between *S. a. aguabonita* and *S. gairdneri,* and the few observable differences (Table 8) can easily be attributed to sampling errors because of the small sizes of some samples. Schreck and Behnke (1971) considered a similar data set (minus samples from DMC and USSC) and proposed synonomy of *S. "whitei"* and *S. g. gilberti.* They referred both to *S. aguabonita* because of similarities in karyotype and morphology, and retained the subspecific designation *S. a. gilberti* for Little Kern trout.

Finally, most upper Kern basin trout, including all named forms except *S. (a.) aguabonita,* cannot be distinguished from the redband trout. Although only limited taxonomic data on redband trout are published (Hoopaugh 1974, Gold 1977), the similarities with most Little Kern trout are obvious, and it has been suggested that all Kern basin golden trouts are actually derivatives of an older, more primitive redband phyletic line (Miller 1972, Gold 1977). Schreck and Behnke (1971) cited the similarities between redband trout and their *S. a. gilberti* as evidence that the latter was not of hybrid origin.

TABLE 8. Meristic Comparisons Among Upper Kern and Other Western *Salmo*.

Character Group	*Pyloric caecae*	*Vertebrae*	*Scales, lateral series*
S. a. aguabonita	21–41 (31.1)* n=141	57–62 (59.6) n=267	150–212 (178.5) n=166
DMC-USSC	24–45 (33.6) n=222	57–63 (60.5) n=222	155–204 (180.1) n=222
Other upper Little Kern trout	23–52 (37.1) n=526	58–65 (61.2) n=526	133–202 (163.6)† n=526
Green Meadows	33–59 (43.7) n=36	59–63 (61.4) n=36	150–191 (162.2) n=36
S. "rosei"	...	60–62 (61.0) n=3	155–170 (162.3) n=3
S. "whitei"	...	60–63 (61.5) n=8	148–167 (159.0) n=8
S. g. gilberti	37–43 (40.0) n=2	60–64 (61.2) n=16	137–160 (152.7) n=10
Redband trout	29–42 (36.0) n=25	60–63 (61.4) n=25	153–174 (162.1) n=25
S. gairdneri	31–79 (50.3) n=246	58–67 (63.0)‡ n=331	115–154 (133.3) n=331

* Data are shown as ranges, means (in parentheses), and sample sizes. Sources of the data were as follows: *S. a. aguabonita* (*S. "roosevelti"* and *S. a. aguabonita* in Table 2 of Schreck and Behnke (1971), and GTC and SFKR in Gold and Gall (1975*a*) and this paper); DMC-USSC trout (Table 6, this paper); other upper Little Kern and Green Meadows trout (Gold and Gall 1975*a*, this paper); *S. "rosei"*, *S. "whitei"*, and *S. g. gilberti* (types and other specimens from collections in 1893, 1904, and 1923, in Table 2 of Schreck and Behnke (1971)); redband trout (Gold 1977); and *S. gairdneri* (RTS and RTV from this paper, four samples in Gold (1975), samples from the Mt. Whitney and Hot Creek hatcheries in California, and samples from two wild steelhead populations along the northern California coast).

† Includes fine-scaled trout from MSSC.

‡ Includes sample with low vertebral number from Mt. Whitney State Hatchery in California.

The picture which emerges is that at least two forms may be identified among past and present upper Kern basin trout: a fine-scaled, low to intermediately spotted, brilliantly colored form represented by Jordan's *S. (a.) aguabonita;* and a second type, which is essentially identical to present-day redband trout, represented by Jordan's *S. g. gilberti,* Evermann's *S. whitei,* and Jordan and McGregor's *S. rosei.* The presence of the first type in both upper Kern and Little Kern waters and at sites located on the southern-most edge of the last glacial advance (Matthes 1965, Schreck 1969: map 4), suggests it is the ancestral form and is descended from among the first trouts to enter the Kern basin either before or during the last glacial retreat. The intermediateness of the second type between *S. a. aguabonita* and *S. gairdneri* suggests a hybrid origin. Stocking records compiled by Schreck (1969) indicate that several introductions and transplants in the upper Kern basin occurred well before Evermann's Little Kern and Kern River collections in 1904, and probably before the 1893 Kern River collections of *S. g. gilberti.* Many of the introductions involved non-natives such as *S. gairdneri* and *S. clarki* (cutthroat trout), and it may be assumed that subsequent transplants often included hybrids between non-natives and endemics.

An alternative view (Schreck and Behnke 1971) is that the *gilberti*-like trout represent a distinct evolutionary lineage which arose either directly from *S. (a.) aguabonita* in the Kern basin, or from a redband-like trout that entered the Kern

at a later time. Geographic considerations do not rule out either possibility since several natural barriers which could engender isolation exist throughout the Kern basin, and infiltration into the Kern by derivatives of the redband trout apparently did occur through adjacent connections in the Sacramento and San Joaquin Valleys.

Our evidence to date suggests that DMC-USSC trout are best referred to *S. (a.) aguabonita,* and that they represent relics of (one of) the earliest trout forms to enter present-day Kern basin waters. Our data unfortunately do not resolve the question of whether other Little Kern basin trout and (by inference) the forms described as *S. g. gilberti* and *S. whitei* merit separate taxonomic status, or whether they represent remnants of hybridization between endemic goldens (*S. (a.) aguabonita*) and introduced (or invading) non-natives. We agree with Behnke (pers. commun.) and Schreck and Behnke (1971) that: (i) many present-day Little Kern trout and those described as *gilberti* and *whitei* are morphologically the same, (ii) this form resembles present-day redband trout, and (iii) more than one trout form probably infiltrated post-glacial Kern basin waters. The problem is that we have not as yet found a consistent, objective criterion for delineating hybrid or introgressed Kern basin trout from those which might represent "pure" *gilberti.* This problem is further confounded by the possibility that introduced (or invading) trout were very likely a heterogeneous mixture of several forms. What is needed in the future are comparative studies using higher resolution genetic techniques (e.g., chromosome banding or DNA sequencing) which will permit direct tests of the hypothesis that Little Kern trout other than those in DMC-USSC warrant separate taxonomic status from the trout originally described as *Salmo aguabonita* Jordan. Electrophoretic studies to determine the amount of biochemical-genetic differentiation between DMC-USSC trout and those recognized as *S. a. aguabonita* are currently in progress.

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APPENDIX TABLE 1. Key to Geographic Locations of Collection Sites.

Collection site	*Longitude W(118°)*	*Latitude N(36°)*	*Altitude (in feet)*
Little Kern River (LKR-1)	33'8"	22'12"	8,800
Little Kern River (LKR-2)	32'56"	21'52"	8,540
Little Kern River (LKR-3)	33'5"	21'12"	8,080
Little Kern River (LKR-4)	31'48"	19'24"	7,200
Upper Shotgun Creek (USGC)	31'48"	22'28"	9,880
Lower Shotgun Creek (LSGC)	31'55"	20'48"	7,720
Rifle Creek (RC)	31'15"	20'8"	7,520
Upper Wet Meadows Creek (UWMC)	34'42"	21'14"	9,200
Lower Wet Meadows Creek (LWMC)	33'48"	21'8"	8,720
Deadman Creek (DMC)	34'8"	20'14"	8,480
Middle Soda Spring Creek (MSSC)	33'50"	18'58"	7,760
Lower Soda Spring Creek (LSSC)	31'25"	15'34"	6,400
Tamarack Creek (TMC)	29'35"	18'48"	7,840
Green Meadows (GM)*	35'53"	20'26"	9,320

*Sample from the South Fork Kaweah River (cf. text).

APPENDIX TABLE 2*a*. **Observed Means, Standard Deviations, and Ranges for Seven Samples of Trout from the Little Kern River Basin Area. Numbers in Parentheses Below Sample Localities Refer to Sample Sizes.**

Character	*LKR-1* (37)	*LKR-2* (40)	*LKR-3* (33)	*LKR-4* (41)	*USGC* (34)	*LSGC* (31)	*RC* (35)
Fork length (cm)	15.0 ± 3.1 (11.0–21.4)	14.1 ± 1.9 (10.6–16.6)	13.6 ± 2.4 (10.4–21.3)	13.3 ± 2.1 (9.1–20.2)	14.6 ± 1.9 (11.4–18.7)	14.0 ± 2.3 (10.2–18.3)	14.7 ± 3.0 (10.6–22.1)
Pyloric caecae	35.86 ± 4.45 (28–45)	36.78 ± 4.44 (31–47)	37.39 ± 5.54 (26–48)	39.32 ± 5.06 (30–50)	36.79 ± 5.46 (30–52)	38.55 ± 4.53 (32–51)	37.29 ± 5.02 (30–52)
Dorsal rays	12.57 ± 0.69 (11–14)	12.78 ± 0.95 (11–14)	12.58 ± 0.71 (11–14)	12.29 ± 0.59 (11–13)	12.32 ± 0.73 (11–14)	12.35 ± 0.75 (11–14)	12.69 ± 0.80 (12–15)
Anal rays	11.14 ± 0.53 (10–12)	11.08 ± 0.47 (10–12)	10.94 ± 0.50 (10–12)	11.10 ± 0.49 (10–12)	11.00 ± 0.60 (10–12)	11.06 ± 0.44 (10–12)	11.37 ± 0.55 (11–13)
Pectoral rays	14.76 ± 0.55 (14–16)	15.30 ± 0.78 (13–17)	15.61 ± 0.79 (14–17)	15.59 ± 0.77 (14–17)	15.41 ± 0.69 (14–17)	15.61 ± 0.66 (15–17)	15.09 ± 0.61 (14–16)
Pelvic rays	9.78 ± 0.48 (9–10)	9.78 ± 0.42 (9–10)	9.79 ± 0.48 (9–11)	9.63 ± 0.49 (9–10)	9.47 ± 0.51 (9–10)	9.71 ± 0.53 (9–11)	9.77 ± 0.41 (9–10)
Branchiostegal rays (total)	23.22 ± 0.95 (21–25)	23.18 ± 1.09 (21–26)	22.79 ± 1.22 (20–25)	23.32 ± 1.31 (21–26)	23.29 ± 0.98 (22–26)	23.00 ± 1.38 (18–25)	22.86 ± 1.18 (20–25)
Vertebrae	61.62 ± 0.92 (60–63)	61.50 ± 1.23 (59–65)	61.55 ± 1.03 (60–64)	61.10 ± 0.94 (59–63)	60.41 ± 0.90 (59–62)	61.03 ± 0.76 (59–62)	60.80 ± 0.83 (59–63)
Gill rakers (left)	20.49 ± 1.12 (18–23)	20.53 ± 1.34 (17–23)	20.58 ± 1.30 (18–24)	20.27 ± 1.02 (19–22)	20.71 ± 1.33 (18–24)	20.97 ± 1.19 (18–24)	19.86 ± 1.09 (17–22)
Scales in lateral series	155.5 ± 8.1 (140–174)	162.4 ± 7.4 (148–176)	164.5 ± 8.5 (151–182)	161.4 ± 8.2 (145–181)	160.5 ± 10.7 (137–188)	165.2 ± 6.6 (153–181)	165.4 ± 8.6 (151–184)
Interneurals	14.51 ± 0.69 (14–16)	14.78 ± 0.89 (13–16)	14.73 ± 0.80 (13–16)	14.49 ± 0.95 (13–16)	14.32 ± 0.88 (13–16)	14.81 ± 0.75 (14–17)	15.06 ± 0.87 (14–17)
Interhaemals	12.30 ± 0.66 (11–13)	12.15 ± 0.86 (10–16)	12.24 ± 0.66 (11–14)	12.12 ± 0.78 (10–14)	12.00 ± 0.74 (11–14)	12.32 ± 0.54 (12–14)	12.54 ± 0.56 (12–13)
Epurals	2.65 ± 0.48 (2–3)	2.70 ± 0.46 (2–3)	2.70 ± 0.47 (2–3)	2.68 ± 0.47 (2–3)	2.73 ± 0.45 (2–3)	2.77 ± 0.42 (2–3)	2.54 ± 0.50 (2–3)
Parr marks	9.66 ± 1.03 (8–12)	9.58 ± 0.87 (8–12)	9.67 ± 0.99 (8–12)	10.00 ± 0.77 (8–11)	10.35 ± 0.80 (9–12)	9.69 ± 1.15 (8–12)	9.87 ± 0.94 (8–12)

APPENDIX TABLE 2*b*. Observed Means, Standard Deviations, and Ranges for Seven Samples of Trout from the Little Kern River Basin Area. Numbers in Parentheses Below Sample Localities Refer to Sample Sizes.

Character	*UWMC (38)*	*LWMC (35)*	*DMC (34)*	*MSSC (39)*	*LSSC (31)*	*TMC (40)*	*GM (36)*
Fork length (cm)	14.6 ± 2.6 (9.2–20.5)	13.3 ± 2.1 (10.9–19.4)	12.5 ± 2.5 (8.2–19.7)	13.0 ± 2.4 (8.8–18.3)	14.5 ± 2.3 (10.0–20.3)	14.1 ± 1.9 (10.7–18.1)	14.8 ± 1.7 (11.0–18.9)
Pyloric caecae	36.16 ± 3.73 (28–44)	38.83 ± 4.35 (30–48)	33.24 ± 3.34 (25–43)	35.97 ± 4.99 (26–47)	37.52 ± 4.54 (31–46)	39.68 ± 4.58 (28–48)	43.67 ± 6.72 (33–59)
Dorsal rays	12.29 ± 0.56 (11–13)	12.46 ± 0.61 (12–13)	12.15 ± 0.50 (11–13)	12.05 ± 0.51 (11–13)	12.06 ± 0.63 (11–13)	12.15 ± 0.70 (10–13)	12.11 ± 0.71 (11–14)
Anal rays	10.97 ± 0.54 (10–12)	11.34 ± 0.54 (10–12)	10.68 ± 0.47 (10–11)	10.90 ± 0.31 (10–11)	11.10 ± 0.47 (10–12)	11.03 ± 0.48 (10–12)	10.83 ± 0.61 (10–12)
Pectoral rays	14.79 ± 0.66 (13–16)	15.69 ± 0.53 (15–17)	15.68 ± 0.52 (14–16)	15.33 ± 0.58 (14–16)	15.16 ± 0.58 (14–16)	15.80 ± 0.65 (15–17)	14.97 ± 0.61 (14–16)
Pelvic rays	9.39 ± 0.50 (9–10)	9.54 ± 0.50 (9–10)	9.00 ± 0.70 (8–10)	9.51 ± 0.51 (9–10)	9.71 ± 0.46 (9–10)	9.60 ± 0.49 (9–10)	9.67 ± 0.48 (9–10)
Branchiostegal rays (total)	22.97 ± 1.39 (21–26)	23.83 ± 1.04 (21–26)	23.91 ± 0.91 (21–25)	22.97 ± 0.84 (21–25)	22.13 ± 1.38 (19–25)	23.08 ± 1.37 (21–26)	23.56 ± 1.40 (22–28)
Vertebrae	60.97 ± 0.86 (60–63)	61.31 ± 0.87 (59–63)	60.06 ± 0.61 (59–61)	61.05 ± 0.86 (60–63)	61.26 ± 0.89 (59–63)	61.18 ± 0.87 (59–63)	61.42 ± 0.87 (59–63)
Gill rakers (left)	19.50 ± 1.12 (18–21)	19.91 ± 0.95 (18–22)	19.97 ± 1.07 (18–22)	20.31 ± 1.15 (18–22)	20.13 ± 1.06 (18–23)	20.38 ± 0.89 (19–22)	19.94 ± 1.12 (18–23)
Scales in lateral series	166.3 ± 8.1 (152–182)	174.1 ± 7.3 (160–189)	183.5 ± 6.9 (170–203)	175.8 ± 9.4 (161–202)	161.2 ± 7.6 (144–180)	166.7 ± 7.7 (151–181)	166.2 ± 10.5 (146–191)
Interneurals	14.29 ± 0.73 (13–15)	14.63 ± 0.81 (13–16)	13.82 ± 0.72 (13–15)	14.33 ± 0.70 (13–15)	14.13 ± 0.81 (12–15)	14.45 ± 0.68 (13–16)	13.81 ± 0.79 (12–15)
Interhaemals	12.16 ± 0.64 (11–14)	12.83 ± 0.57 (12–14)	11.71 ± 0.46 (11–12)	11.95 ± 0.56 (11–13)	12.45 ± 0.67 (11–14)	12.15 ± 0.73 (11–14)	11.75 ± 0.69 (10–13)
Epurals	2.71 ± 0.46 (2–3)	2.83 ± 0.38 (2–3)	2.97 ± 0.17 (2–3)	2.79 ± 0.41 (2–3)	2.77 ± 0.50 (2–4)	2.72 ± 0.45 (2–3)	2.86 ± 0.42 (2–4)
Parr marks	9.97 ± 0.98 (8–12)	10.03 ± 0.71 (9–12)	11.25 ± 0.80 (9–13)	10.53 ± 0.99 (8–12)	10.18 ± 0.98 (8–12)	9.86 ± 0.72 (8–11)	10.40 ± 0.89 (9–12)

APPENDIX TABLE 3. Observed Means, Standard Deviations, and Ranges for Three Samples of Trout from California. Numbers in Parentheses Below Sample Localities Refer to Sample Sizes.

Character	*SFKR (19)*	*RTV (24)*	*RTS (24)*
Fork length (cm)	12.5 ± 1.7 (8.1–14.7)	23.0 ± 1.0 (20.5–24.5)	23.2 ± 1.9 (19.0–26.3)
Pyloric caecae	31.53 ± 3.60 (26–37)	61.50 ± 8.38 (46–75)	61.36 ± 6.89 (52–79)
Dorsal rays	11.84 ± 0.60 (11–13)	12.37 ± 0.58 (11–13)	12.36 ± 0.49 (12–13)
Anal rays	10.84 ± 0.37 (10–11)	11.08 ± 0.50 (10–13)	11.20 ± 0.41 (11–12)
Pectoral rays	14.47 ± 0.51 (14–15)	14.21 ± 0.59 (13–16)	14.68 ± 0.56 (14–16)
Pelvic rays	9.0 ± 0.0 (9–9)	10.00 ± 0.0 (10–10)	9.92 ± 0.28 (9–11)
Branchiostegal rays (total)	21.00 ± 1.00 (20–23)	21.17 ± 0.76 (20–22)	21.32 ± 1.25 (19–23)
Vertebrae	59.84 ± 0.96 (58–61)	62.46 ± 0.78 (61–64)	63.44 ± 0.65 (62–65)
Gill rakers (left)	19.63 ± 0.76 (18–21)	18.21 ± 1.10 (16–20)	18.04 ± 0.93 (16–19)
Scales in lateral series	172.7 ± 7.7 (164–189)	130.7 ± 5.2 (119–138)	142.2 ± 4.92 (137–151)
Interneurals	13.10 ± 0.81 (12–14)	14.67 ± 0.70 (13–16)	14.68 ± 0.56 (14–16)
Interhaemals	11.95 ± 0.62 (11–13)	12.71 ± 0.62 (12–14)	12.68 ± 0.56 (12–14)
Epurals	2.53 ± 0.51 (2–3)	—	—
Parr marks	9.84 ± 1.12 (8–12)	—	—

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LINGCOD, *OPHIODON ELONGATUS*, SPAWNING AND NESTING IN SAN JUAN CHANNEL, WASHINGTON [1]

MARK G. LARIVIERE [2], DAVID D. JESSUP,
AND STEPHEN B. MATHEWS
College of Fisheries, University of Washington
Seattle, Washington 98195

The spawning season and nest guarding behavior of lingcod, *Ophiodon elongatus*, in San Juan Channel of northern Puget Sound, Washington, began in mid-December and continued through May. Nests were located from 2.4 to 19.8 m below MLLW, usually in crevices or under boulders. Most were attended by a guardian male. Nests were located along transects only where there was a combination of suitable substrate and high currents. Predation by invertebrates was common; vertebrate predation uncommon. It was estimated that 40% of the 35 nests encountered successfully hatched.

INTRODUCTION

Concern over lingcod, *Ophiodon elongatus*, stocks in inside marine waters of Washington State has increased in recent years due to a decline in the abundance of lingcod in Puget Sound and Hood Canal (Ilg, Walton, and Buckley 1979). In 1978 the Washington State Department of Fisheries (WDF) closed southern Puget Sound to commercial and recreational lingcod harvesting, and instituted a winter closure for northern Puget Sound. This closure, currently 1 December to 14 April, is intended to protect the fish from exploitation during their spawning and nesting season. While complete protection was given to southern Puget Sound stocks, it was felt that spawning season protection was adequate for the more abundant northern Puget Sound stocks.

During the winter of 1979–1980, we studied the spawning habits and nesting behavior of lingcod in the San Juan Island area of northern Puget Sound. Specifically, we sought to determine if the winter closure coincided with lingcod spawning and nesting activities. More generally, we wished to add to the recorded observations on territorial behavior of nest guarding males, distribution of nests by depth and substrate, and impact of predation on nests. Understanding the reproductive processes and early life-stage mortalities is fundamental in explaining or predicting population trends.

Previous observations of lingcod spawning and nesting activities include those reported by Jewell (1968) for southern Puget Sound and Low and Beamish (1978) for the Strait of Georgia.

METHODS AND MATERIALS

Scuba surveys were conducted at three study areas in San Juan Channel near the Friday Harbor Laboratories of the University of Washington: Shady Cove and North Cove on San Juan Island, and the northeast tip of Turn Island (Figure 1). Surveys by the first two authors during the winter of 1978–79 and reports from earlier investigators (Moulton 1977) indicated lingcod used these locations for spawning and nesting. A total of 17.5 h of observations was conducted on 36 dives between 1 October 1979 and 31 May 1980.

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[2] Current address: Friday Harbor Laboratories, Friday Harbor, Washington 98250.

FIGURE 1. Location of study sites.

Dives were made from a boat at slack water. Study depths ranged from 0 to 24.3 m below mean lower low water (MLLW). A 100-m steel transect line was established at a depth of 13.7 m to aid in orientation of the divers to the substrate and to delimit each study area. All nests encountered were marked by leaving a numbered yellow rock in a nearby conspicuous location. On all dives we attempted to relocate previously marked nests as well as to find new nests.

Each nest was evaluated as to stage of egg development (pink = fresh; white = intermediate age; gray = near hatching), extent of vertebrate or invertebrate predation, and reduction in size of egg mass from hatching or predation. Nests were categorized as follows: (i) in crevice on cliff face; (ii) under boulders greater than 2 m; (iii) under boulders less than 2 m; or (iv) not attached to substrate (loose). Observations were recorded on slates underwater and transcribed to paper at the end of the day. Depths were measured to the nearest 5-ft interval with oil-filled depth gauges and converted to metres below MLLW from tide tables.

RESULTS

Each of the three study areas has a substrate of vertical cliffs at shallow depths (0 to 12.0 m below MLLW) and high relief bedrock at intermediate depths (12.0 to 24.0 m below MLLW). Strong tidal currents (up to 4.6 km/h) sweep the more exposed sections of the transects. Sea surface temperatures range annually from 7 to 11°C.

Territoriality

Territorial defense by male lingcod was first noted in October at Shady Cove and North Cove and in December at Turn Island. When disturbed, the fish would circle tightly and settle to the bottom nearby. As the spawning season progressed and the fish began active nest defense, they became less and less wary of the divers, allowing limited handling and very close observation.

Some aggressive lingcod were encountered. Several times this behavior was quite antagonistic and precluded observations closer than about 2 m from the nest. These incidences always involved large (80+ cm) guardian male lingcod encountered for the first time; however, antagonistic behavior by such fish tended to diminish on subsequent surveys. Threat displays included gaping of the mouth, flaring of the opercules and pectoral fins, raising the dorsal fin, arching the back, and short charges.

The males remained in their territories until the nest hatched and occasionally after. The fish would position themselves directly over the egg mass or within 1 m. No effort was made to determine territory size, but nests with guardian males were found as close as 2 m to one another. There were two instances of a single male guarding two nests deposited at different times within 0.5 of each other. In another case an egg mass disappeared prior to hatching and the male remained within the territory. Within 3 weeks this fish had acquired a new nest in the same location.

Aeration by fanning of egg masses with pectoral fins as reported by Hart (1973) was never observed. Spawning was not observed during this study. Occasional large (> 100 cm) lingcod were present during daylight hours at each of the study sites. The carcass of a large lingcod of unknown sex was recovered at 3.0 m below MLLW near North Cove on 12 January 1980. Age was 15+ as determined by a vertebral count (Chatwin 1956).

Nesting Activities

The lingcod spawned large, adhesive masses of white to pinkish eggs (averaging 3.5 mm in diameter), depositing them in crevices, caves, and under or between boulders. Often the sites had an opening behind the egg mass to allow for water flow and access by the guardian male. The egg masses conformed to substrate irregularities and sometimes exhibited other irregularities and depressions that seemed the result of contact by the adult lingcod during or shortly after spawning.

The first nest was seen on 16 December and egg deposition continued sporadically until early April. The maximum number of nests seen occurred during late February to early March (Figure 2). Nest depths ranged from 2.4 to 19.8 m below MLLW. No attempt was made to locate nests deeper than 24.3 m during this study.

Turn Island: Of 12 separate nests found, the first appeared on 3 January and the most (9) were seen on 23 February and 1 March. Nest deposition occurred through March; depths ranged from 2.4 to 18.6 m. One nest was guarded by a lingcod tagged (WDF spaghetti tag—TO 2442) and released in the Turn Island area 3 years previously (Mathews *et al.* 1979). This fish remained at the nest until hatching occurred and then disappeared.

TABLE 2. Record of Individual Lingcod Nests and Guardian Males Observed at the San Juan Channel Sites.[1]

Nest No.	Depth [2]	Size of Male (cm)	Dec. 16	Dec. 19	Jan. 3	Jan. 4	Jan. 12	Jan. 13	Jan. 19	Jan. 20	Feb. 2	Feb. 3	Feb. 17	Feb. 23	Mar. 1	Mar. 2	Mar. 8	Mar. 25	Mar. 26	Mar. 27	Apr. 12	Apr. 19	Apr. 20	Apr. 26	May 4	May 17	May 31	Status of Nest [4]
Shady Cove																											
SC-1a	14.7	80				Ⓣ		T																			dh
SC-1b	14.7	80									Ⓣ			Ⓣ		Ⓣ				T							ph
SC-2	14.2	65						Ⓣ		0	Ⓣ			Ⓣ		Ⓣ				T							h
SC-3	13.5	65								Ⓣ				Ⓣ		T											ph
SC-4	14.3	70									Ⓣ			T													dh
SC-5	5.9	70									Ⓣ			Ⓣ												T	u
SC-6	5.1	60									0					Ⓣ				Ⓣ		T					ph
SC-7	19.8	75												Ⓣ		Ⓣ				Ⓣ		T					u
SC-8a	14.9	80												Ⓣ		Ⓣ				Ⓣ		T					u
SC-8b	14.9	80														Ⓣ				Ⓣ		T					u
SC-9	15.7	65												Ⓣ		Ⓣ						T					u
SC-10	13.7	75														Ⓣ						T					u
SC-11	17.1	65														Ⓣ										T	u
SC-12	7.9	65														Ⓣ				T		T					u
Turn Island																											
TI-1	6.1	70			Ⓣ				Ⓣ			Ⓣ		T													ph
TI-2	14.5	100							0			Ⓣ		Ⓣ	T												ph
TI-3a	12.9	65							Ⓣ			Ⓣ		Ⓣ	T												ph
TI-3b	12.9	65												Ⓣ	Ⓣ			Ⓣ			T						ph
TI-4	5.9	65							0			0			Ⓣ						T						u
TI-5	15.2	75												0	Ⓣ			T									u
TI-6	15.8	–												0	0			T									u
TI-7	17.4	70												Ⓣ	0			Ⓣ			T						u
TI-8	2.4	–												0	0			T									dh
– [3]	4.8	–												0							T						u
– [3]	11.0	–													0						T						u
TI-9	18.6	70															Ⓣ		Ⓣ		T						ph

North Cove																			
NC-1	5.6	80	Ⓟ	Ⓟ	Ⓟ	T													ph
NC-2	9.8	70		Ⓟ	Ⓟ	Ⓟ		T											ph
NC-3	14.5	75				Ⓟ				Ⓟ						T			u
NC-4	7.6	65				Ⓟ	Ⓟ	Ⓟ		Ⓟ						T			h
NC-5	6.7	85				Ⓟ	Ⓟ	Ⓟ		Ⓟ						T			u
NC-6	7.6	70					Ⓟ	Ⓟ		Ⓟ						T			h
–[3]	15.5	–						0								T			u
–[3]	17.1	70								Ⓟ						T	Ⓟ	Ⓟ	u
NC-11	12.5	95													Ⓟ	Ⓟ	Ⓟ	Ⓟ	ph

[1] Format of table follows Jewell (1968)
[2] meters below MLLW
[3] unmarked nest
[4] h — hatched; ph — probably hatched; u — unknown; dh — did not hatch

Symbols:
0 — nest observed, no male
Ⓟ — nest with male
T — nest gone
blank — nest not observed

North Cove: Of nine nests, the first appeared on 16 December and peak nesting occurred on 25 March with five guarded nests present. Nest deposition occurred through April. One guarded nest was present in the study site area until 17 May. Depths ranged from 5.6 to 17.1 m.

Shady Cove: Fourteen nests were observed at Shady Cove. The first appeared 4 January and peak nesting occurred on 2 March with 11 nests present. Nest deposition occurred until 2 March and males were present on nests until early April. Depths ranged from 5.1 to 19.8 m.

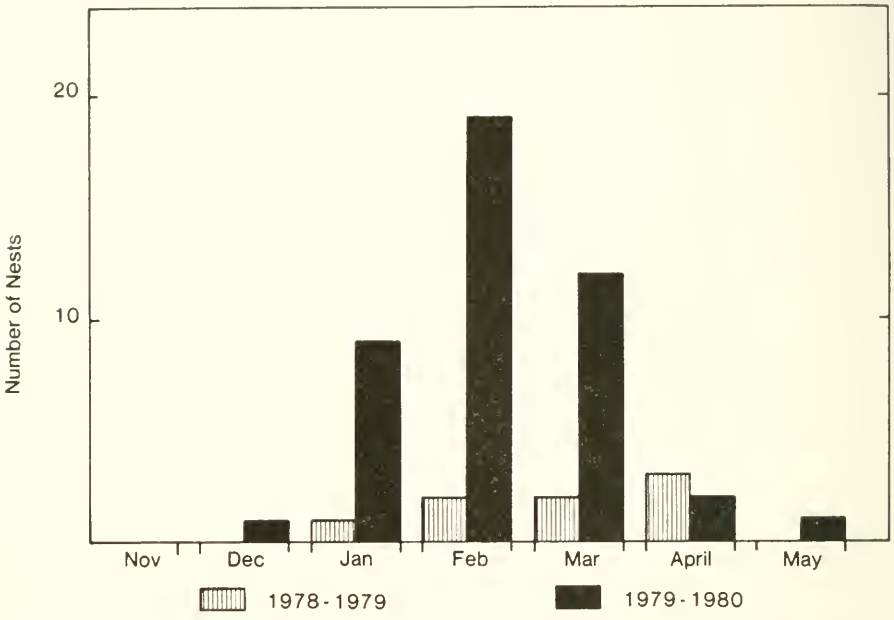

FIGURE 2. Number of lingcod nest sitings by month.

Predation

Most nests incurred some form of predation, usually by invertebrates feeding upon the exposed peripheral layer of eggs. Diatom flora was present on many of the egg masses during later stages of development.

Guarded, unguarded, and loose nests had present upon them one or both of the gastropods *Amphissa columbiana* and *Calliostoma ligatum.* No active defense of the nest against these organisms was observed, although the stomachs of several male lingcod examined in the sport fishery during another study in the spring of 1979 and 1980 contained several *Amphissa* sp. and *Callistoma* sp. as well as some lingcod eggs. Moulton (1977) also found these two gastropods in the stomachs of lingcod recovered by hook and line in the winter period.

Predators observed upon guarded nests were hermit crabs, *Pagurus* sp., the sharp-nose crab, *Scyra acutifrons,* the scalyhead sculpin, *Artedius harringtoni,* and the Puget Sound rockfish, *Sebastes emphaeus.* Predators observed on unguarded nests included the red sea urchin, *Strongylocentrotus franciscanus,* the purple sea urchin, *S. purpuratus,* hermit crabs, and some small unidentified

shrimp. Unguarded nests free on the bottom were preyed upon by the red and purple sea urchins and small shrimp. Sightings of predators on guarded and unguarded nests were not as common as sightings of gastropods upon the nests (Table 1).

TABLE 1. Organisms Preying on Lingcod Egg Masses. Each Sighting Documents the Occurrence of One or More Individuals on an Egg Mass on a Specific Survey Date.

	Number of sightings		
Organism	*Guarded egg masses*	*Unguarded egg masses*	*Totals*
Amphissa columbiana	30	5	35
Calliostoma ligatum	15	1	16
Cottidae	5	0	5
Pagurus sp.	3	1	4
Stronglylocentrotus franciscanus	0	3	3
Caridea (shrimp)	2	1	3
Stronglylocentrotus purpuratus	0	2	2
Sebastes emphaeus	2	0	2
Artedius harringtoni	1	0	1
Scyra acutifrons	1	0	1
Phyllolithodes pepillosus	1	0	1
No predation	17	0	17

Guardian lingcod were not seen to respond to the gastropods, shrimp, or small fish, but were observed to chase away larger fish and, in one case, to pick a sharp-nose crab from an egg mass. No attempts were made to collect guardian males and examine the stomach contents for predators.

Hatching

Three egg masses were observed to hatch; the cause of the disappearance of the others had to be inferred. We judged that hatching occurred in 11 other nests, as evidenced by the stage of egg development when the nest was first seen, presence of guardian male, apparent insignificant predation, and total time span observed (Table 2).

DISCUSSION

Lingcod nesting in the San Juan Island area of northern Puget Sound extends from mid December through May. Viable nests may be present into June, but most eggs have hatched by mid April. These dates extend the length of the nesting season about 1 month later than previously determined for Washington State waters (Jewell 1968). It appears the winter closure is adequate for protection of the spawning and nesting fish in northern Puget Sound waters.

The lingcod spawned only in crevices or caves on rocky substrate where the current was relatively high (up to 4.6 km/h) along each of our transects. Since lingcod prefer a combination of high currents and suitable crevices for nest deposition, spawning success is probably related to the availability of both of these factors. Current is needed to assure oxygenation throughout the egg mass, and fissures or crevices are needed to insure adhesion in the current. Nests were not found where currents tended to be low or deflected, nor on the coarse gravel slopes, open boulder fields, or vertical cliff faces without crevices. Phillips (1959), Jewell (1968), and Low and Beamish (1978) all indicate the necessity of proper substrate and sufficient water movement for successful lingcod spawning.

Aeration of the egg mass is probably accomplished by tidal flow rather than by nest-guardian fanning. Fanning is reported for other closely related demersal egg brooding fish in Puget Sound (DeMartini and Patten 1979) and in earlier literature for lingcod (Wilby 1937, Hart 1973). It is significant that neither we nor Low and Beamish (1978) observed aeration of lingcod egg masses by guardian males.

Maximum depth at which a nest was encountered was 19.8 m. Moulton (1977) reported a nest of 20.4 m below MLLW at Shady Cove. The substrate below 24 m at each of the study areas was a gradually sloped, gravelly bottom with little or no boulder cover. Little effort was expended in trying to locate nests in these areas. The presence of a nest seems to be more dependent upon availability of suitable substrate than a function of depth. It is conceivable that lingcod nests occur at depths below 20 m in the San Juan Islands. Miller and Geibel (1973) speculate that lingcod nest guardians may be found as deep as 73 m in California waters.

The limitations of this study did not allow us to determine precisely the impact of predation on lingcod egg masses. Enough observations were made to list significant invertebrate predators (Table 1), but too little time was spent underwater to assess vertebrate predator impacts. One finding of note is that loose or unguarded egg masses are much more vulnerable to invertebrate predation; they were more likely to disappear in the weekly intervals between our dives than attached, guarded egg masses.

Some nest disappearances could be attributed to dislodging by the current. Such nests would become subject to intense predation as they wash loosely along the bottom. Low and Beamish (1978) observed kelp greenling, *Hexagrammos decagrammus;* striped seaperch, *Embiotoca lateralis*; and the sunflower starfish, *Pycnopodia helianthoides,* preying on lingcod eggs: all were common in our study areas, but we did not see these species feeding on egg masses.

Predation on guarded nests in crevices and caves was restricted to small fish and invertebrates. Often a nest was so placed as to preclude larger invertebrates from reaching it. In several instances a large number of red sea urchins were seen near a nest, but none actually feeding upon the eggs because such nests were in crevices too narrow for the urchins.

Of 35 nests observed in this study, three were known to hatch and 11 others probably hatched, for a 40% hatching success rate. Using similar criteria for hatching success as we, Low and Beamish (1978) concluded that 21 of 77 nests observed (27%) hatched. Our 40% hatching rate may be a minimal estimate, for predation was not extensive on most of the nests which disappeared too soon to judge them successful. Daily observations of the nests during the hatching period would be needed for a more precise estimate of nest hatching success rate.

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LARVAL ANISAKINE ROUNDWORMS OF MARINE FISHES FROM SOUTHERN AND CENTRAL CALIFORNIA, WITH COMMENTS ON PUBLIC HEALTH SIGNIFICANCE [1]

MURRAY D. DAILEY
Southern California Ocean Studies Consortium
and Department of Biology
California State University, Long Beach
Long Beach, California 90840

LAURITZ A. JENSEN
Department of Biology
University of Northern Colorado
Greeley, Colorado 80639

BARBARA WESTERHOF HILL
Southern California Ocean Studies Consortium
925 Harbor Plaza
Long Beach, California 90801

During November 1975 to December 1979, 2,268 marine fishes representing 36 genera and 68 species were collected from southern and central California and examined for larval nematodes (roundworms) of the family Anisakidae. Larvae of the genus *Anisakis* were found in the visceral tissue of 41.6% of the fishes examined, while those of *Phocanema* occurred in visceral tissue of 5.9%. *Phocanema* was also recovered from the muscle tissue of 11 species.

Since humans can become infected by consuming improperly prepared fish harboring muscle roundworms, we suggest that species of fishes known to harbor muscle roundworms not be consumed unless properly prepared.

INTRODUCTION

We conducted a study to determine the prevalence of larval *Anisakis* and *Phocanema* nematodes in local marine fishes in order to learn what impact they might have on human health. Records show that humans can become infected with larval nematodes by eating raw fish such as sashimi (Van Thiel, Kuipers, and Roscam 1960; Chitwood 1970; Davey 1971; Kagei *et al.* 1972; Oshima 1972; Juels *et al.* 1975; Dailey, unpubl. data), salt fish (Pinkus, Coolidge, and Little 1975), and marinated fish such as ceviche (Chitwood 1975).

The adult forms of these worms infect marine mammals, commonly causing ulceration and granulomas in the stomach wall.

MATERIAL AND METHODS

From November 1975 to December 1979, 2,268 fishes representing 36 genera and 68 species were obtained from commercial and sport fishermen. The geographic range was from Monterey to San Diego, California, and included the offshore islands of San Nicolas, San Miguel, Anacapa, Santa Cruz, and Santa Rosa. Fishes were filleted and eviscerated, and examined macroscopically for roundworms. Representative worms were retained and cleared in lactophenol for microscopic examination and identified according to the morphology of the digestive tract (*Phocanema* with intestinal caecum; *Anisakis* without). *Phocanema* (Figure 1) was distinguished grossly from *Anisakis* (Figure 2) by a brown color and loose coil pattern in tissue.

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FIGURE 1. Larvae of *Phocanema* in muscle of *Sebastes serranoides*. Note loose coil. *Photograph by L. Jensen.*

FIGURE 2. Larvae of *Anisakis* in liver of *Synodus lucioceps*. Note tight coil. *Photograph by L. Jensen.*

RESULTS

Larvae of *Anisakis* were found in 943 (41.6%) fishes, and larvae of *Phocanema* in 134 (5.9%) fishes (Table 1). The number of *Anisakis* larvae ranged from 1 to 268 per fish and were recovered only from visceral tissue. *Phocanema* larvae were recovered from both viscera and muscle, and ranged from 1 to 20 per fish in viscera, and 1 to 15 per fish in muscle. *Phocanema* was found in the muscle tissue of only *Sebastes paucispinis, S. rastrelliger, S. serranoides, S. chlorostictus, Ophiodon elongatus, Atherinopsis californiensis, Synodus lucioceps, Paralabrax nebulifer, Anoplopoma fimbria, Paralichthys californicus,* and *Genyonemus lineatus.*

DISCUSSION

We found that many California marine fishes are infected with larval anisakine worms. Records reveal that the highest incidence of human infection is a result of eating undercooked or marinated fish. The infection (anisakiasis) may be lumenal in nature, where no tissue penetration occurs, and the worms are coughed up, vomited, or expelled in the feces (Chitwood 1975; Juels *et al.* 1975). The worms may also penetrate digestive tract tissue and surgery is required for their removal.

Two types of anisakiasis are recognized: gastric and intestinal (Smith and Wootten 1978). Stomach pains, nausea, and vomiting 4 to 6 h after consumption of sea food is characteristic of acute gastric infections. Chronic manifestations of stomach involvement include eosinophilia, occult blood in stool, and penetration of the stomach wall. The intestinal form is detectable within 7 d after eating infected fish, and the symptoms are marked with abdominal pain, nausea, vomiting, diarrhea, and occult blood in the stool. These invasive forms may mimic appendicitis, cancer, or intestinal obstruction; hence it is possible that many cases are misdiagnosed and not reported.

The impact of the larval anisakine infected fishes on public health depends on whether the infected fishes are adequately frozen and properly prepared for consumption.

To eliminate human infection, fish to be consumed should be candled, cooked at temperatures above 60°C, or frozen to −20°C for at least 24 h (Dailey 1975, Smith and Wootten 1978). Since anisakine larvae may be resistant to marinades, brines, and smoking procedures, we suggest that species of fish known to harbor muscle roundworms not be consumed if prepared by the latter methods.

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TABLE 1. California Marine Fishes with *Anisakis* and/or *Phocanema* Larvae

Species			Fishes with *Anisakis*		No. *Anisakis* per fish	Fishes with *Phocanema*			No. *Phocanema* per fish
Scientific name	Common name	No. Examined	No.	%	(range)	No.	%	No. with muscle envolvement	(range)
Sebastes miniatus	Vermilion rockfish	69	31	44.9	1–44	19	27.5	0	1–15
Sebastes mystinus	Blue rockfish	68	0	0	0	0	0	0	0
Sebastes chrysomelas	Black-and-yellow rockfish	1	0	0	0	0	0	0	0
Sebastes ovalis	Speckled rockfish	3	1	33.3	1	0	0	0	0
Sebastes paucispinis	Bocaccio	449	356	79.2	1–268	9	2	6	1
Sebastes phillipsi	Chameleon rockfish	1	1	100	1	0	0	0	0
Sebastes rosenblatti	Greenblotched rockfish	3	1	33.3	1	0	0	0	0
Sebastes rastrelliger	Grass rockfish	16	2	12.5	1	1	6.3	1	1
Sebastes rosaceus	Rosy rockfish	51	5	9.8	1–2	0	0	0	0
Sebastes carnatus	Gopher rockfish	2	0	0	0	0	0	0	0
Sebastes serranoides	Olive rockfish	44	4	9	1–4	2	4.5	2	6–15
Sebastes caurinus	Copper rockfish	22	0	0	0	1	4.4	0	1
Sebastes flavidus	Yellowtail rockfish	16	0	0	0	0	0	0	0
Sebastes atrovirens	Kelp rockfish	19	5	26.3	1–2	0	0	0	0
Sebastes rufus	Bank rockfish	39	3	7.7	1–4	0	0	0	0
Sebastes auriculatus	Brown rockfish	16	14	87.5	1–7	0	0	0	0
Sebastes rubrivinctus	Flag rockfish	13	2	15.4	1–2	0	0	0	0
Sebastes chlorostictus	Greenspotted rockfish	140	28	20	1–10	7	5	1	1–4
Sebastes dalli	Calico rockfish	27	0	0	0	0	0	0	0
Sebastes melanops	Black rockfish	2	0	0	0	0	0	0	0
Sebastes diploproa	Splitnose rockfish	2	2	100	1–4	0	0	0	0
Sebastes elongatus	Greenstripped rockfish	38	6	15.9	1–3	0	0	0	0
Sebastes nebulosus	China rockfish	2	0	0	0	0	0	0	0
Sebastes entomelas	Widow rockfish	1	0	0	0	0	0	0	0
Sebastes serriceps	Treefish	5	1	20	2	0	0	0	0
Sebastes goodei	Chilipepper	191	123	64.4	1–7	0	0	0	0
Sebastes gilli	Bronzespotted rockfish	5	3	60	1–81	2	40	0	1–3
Sebastes hopkinsi	Squarespot rockfish	13	1	7.7	1	0	0	0	0
Sebastes levis	Cowcod rockfish	34	7	20.6	1–200	0	0	0	0
Sebastes macdonaldi	Mexican rockfish	2	2	100	2–9	0	0	0	0
Sebastes constellatus	Starry rockfish	25	4	16	1	0	0	0	0

Sebastes pinniger	Canary rockfish	4	0	0	0	0	0	0	0
Scorpanenichthys marmoratus	Cabezon	4	0	0	0	0	0	0	0
Hexagrammos decagrammus	Kelp greenling	1	0	0	0	0	0	0	0
Ophiodon elongatus	Lingcod	19	1	5.3	1	2	10.5	2	1
Scorpaena guttata	California scorpionfish	23	4	17.4	1–4	0	0	0	0
Pleuronichthys verticalis	Hornyhead turbot	2	0	0	0	0	0	0	0
Parophrys vetulus	English sole	1	0	0	0	0	0	0	0
Hippoglossina stomata	Bigmouth sole	2	1	50	3	0	0	0	0
Citharichthys sordidus	Pacific sanddab	35	14	40	1–5	1	2.9	0	1
Atherinopsis californiensis	Jacksmelt	12	6	50	1–3	4	33.3	4	1–5
Sphyraena argentea	Pacific barracuda	4	0	0	0	0	0	0	0
Synodus lucioceps	California lizardfish	331	177	53.5	1–11	35	10.6	7	1–8
Paralabrax clathratus	Kelp bass	180	22	12.2	1–33	27	15	0	1–17
Paralabrax nebulifer	Barred sand bass	16	11	68.8	1–12	9	56.3	3	1–7
Anoplopoma fimbria	Sablefish	18	3	16.7	1–16	3	16.7	1	1–18
Caulolatilus princeps	Ocean whitefish	12	0	0	0	0	0	0	0
Seriola dorsalis	Yellowtail	4	0	0	0	0	0	0	0
Amphistichus koelzi	Calico surfperch	1	0	0	0	0	0	0	0
Hypsurus caryi	Rainbow surfperch	1	0	0	0	0	0	0	0
Rhacochilus toxotes	Rubberlip surfperch	1	0	0	0	0	0	0	0
Medialuna californiensis	Halfmoon	9	0	0	0	0	0	0	0
Girella nigricans	Opaleye	2	0	0	0	0	0	0	0
Heterostichus rostratus	Giant kelpfish	1	0	0	0	0	0	0	0
Semicossphus pulcher	California sheephead	11	1	9.1	3	1	9.1	0	20
Eopsetta jordani	Petrale sole	2	2	100	4	0	0	0	0
Microstomus pacificus	Dover sole	3	0	0	0	0	0	0	0
Paralichthys californicus	California halibut	31	27	87.1	4–12	6	19.4	3	1–3
Platichthys stellatus	Starry flounder	4	1	25	5	0	0	0	0
Anisotremus davidsoni	Sargo	2	0	0	0	0	0	0	0
Cheilotrema saturnum	Black croaker	2	1	50	1	0	0	0	0
Cynoscion nobilis	White seabass	9	8	88.9	2–4	0	0	0	0
Genyonemus lineatus	White croaker	100	25	25	1–6	5	5	5	1–2
Menticirrhus undulatus	California corbina	3	0	0	0	0	0	0	0
Seriphus politus	Queenfish	2	2	100	1–7	0	0	0	0
Sarda chiliensis	Pacific bonito	30	9	30	1–6	0	0	0	0
Scomber japonicus	Chub mackerel	55	14	25.5	1–8	0	0	0	0
Merluccius productus	Pacific hake	12	12	100	1–16	0	0	0	0

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EVIDENCE OF MOVEMENTS OF SOME DEEPWATER ROCKFISHES (SCORPAENIDAE: GENUS *SEBASTES*) OFF SOUTHERN CALIFORNIA [1]

MILTON S. LOVE
Department of Biology
Occidental College
1600 Campus Road
Los Angeles, California 90041

Evidence is presented for movements of some rockfishes in deepwater (greater than 70 m) off southern California. Data taken during an 11-month period from sportfish partyboats indicate large fluctuations in catch-per-unit-effort of three rockfish species (*Sebastes entomelas, S. miniatus,* and *S. paucispinis*) from a single rocky reef. Further, on two occasions, movements (of up to 2.4 km a day) of rockfish aggregations were noted, based on echo location and hook-and-line sampling. Species taken from the aggregations included *S. entomelas, S. goodei, S. levis, S. miniatus,* and *S. paucispinis.*

INTRODUCTION

Rockfishes (Scorpaenidae: Genus *Sebastes*) are an important constituent of the California marine fish assemblage and are a mainstay of the California sport and commercial fishing industries (McAllister 1976).

Studies of shallow-dwelling nearshore rockfishes in the northeastern Pacific (summarized by Love 1978) indicate that, with the exception of *S. melanops,* the black rockfish, inshore rockfishes exhibit restricted movements. Movements of deeper water species (inhabiting depths below 70 m) are less well known, as direct observation is difficult and tagging has not been effective.

While conducting two studies, neither directly related to rockfish movements, I accumulated evidence that some deeper water rockfishes may move about extensively.

From April 1975 through July 1978, I conducted a survey of the partyboat sportfishery off Santa Barbara, California (lat. 34°30'N; long. 119° 40'W). Once or twice per week I sampled aboard the sportfishing vessels, identifying and counting all fishes brought aboard. While analyzing the results of the survey, my attention was drawn to catch data from one particular reef. The reef was originally located by a partyboat operator in September 1977 and was fished every month through the end of the study. Composed of 1–3 m high rocky substrate, surrounded by sand and mud, the reef is situated at a depth of 96 m about 10 km SSW of Santa Barbara Harbor. Extensive echo-soundings indicate that the nearest adjacent reef is in 140 m, about 2 km to the west.

Catch-per-unit-effort of the three most commonly taken species, *S. paucispinis* (bocaccio), *S. miniatus* (vermilion rockfish), and *S. entomelas* (widow rockfish), fluctuated throughout the year (Table 1). *S. paucispinis* and *S. miniatus* were taken during every month, though few *S. paucispinis* were taken in the November through January period and in June; and the low points in the *S. miniatus* catch were November through February and July. *S. entomelas* were only taken during May and June. Other species were taken in smaller numbers through most months.

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TABLE 1. Partyboat Catch-Per-Unit-Effort * of Eight Rockfish Species, from a Reef off Santa Barbara, California, from September 1977 through July 1978. Actual Species Catch Per Month in Parentheses.

	Sept.	*Oct.*	*Nov.*	*Dec.*	*Jan.*	*Feb.*	*Mar.*	*Apr.*	*May*	*June*	*July*
S. paucispinis	7.2(547)	5.5(363)	tr **(6)	tr(1)	tr(1)	11.2(974)	8.3(647)	6.1(436)	9.1(928)	tr(2)	5.2(255)
S. entomelas	—	—	—	—	—	—	—	—	2.7(275)	3.6(259)	—
S. miniatus	.3(23)	.6(40)	tr(7)	tr(4)	tr(3)	tr(1)	7.1(653)	6.4(556)	8.2(639)	1.7(111)	tr(1)
S. chlorostictus	tr(6)	.1	.1	.3	.2	tr(4)	tr(4)	tr(2)	.1	.3	tr(2)
S. rubrivinctus	tr(1)	tr(3)	tr(3)	tr(2)	—	tr(4)	tr(3)	tr(1)	tr(1)	tr(1)	tr(1)
S. levis	—	—	tr(1)	tr(2)	—	—	tr(1)	—	tr(1)	tr(1)	tr(1)
S. elongatus	tr(2)	tr(3)	tr(3)	tr(3)	tr(2)	tr(1)	tr(3)	tr(3)	tr(6)	—	tr(2)
S. pinniger	—	—	—	—	—	—	—	tr(1)	—	—	—
Samples	4	4	4	4	4	3	4	5	5	4	3
Anglers	76	66	81	97	92	87	78	65	102	72	49

* Catch-Per-Unit-Effort (CPUE) = fish per angler per day
** "Tr" refers to a CPUE of less than 0.1 per day

A second set of observations occurred while sampling rockfishes for a spawning season study. On two occasions I noted substantial movements of deepwater rockfish aggregations. The observations were made on the Twelve Mile Reef, located in the Santa Barbara Channel, about 19 km SSE of Santa Barbara Harbor. The reef, at a depth of 110–220 m, extends for about 16 km along the central axis of the Channel.

In January 1970, using a strip-chart fathometer, I located an aggregation of rockfish in water of about 135 m depth. Fish were detected and angled from the floor to as much as 27 m above the bottom. A buoy was set to mark the aggregation's location and a string of baited hooks was lowered. Successive drifts with hooks over the original location yielded no fish. A search of the area revealed the aggregation some 100 m from the original location. By relocating the aggregation and immediately lowering the hooks, I could catch fish for brief periods before they again moved on. After 7 hours, the fish had moved over 2.4 km from the original site to a new location where the bottom depth was 157 m. Species caught from the aggregation were predominantly *S. paucispinis, S. goodei* and *S. entomelas* along with fewer individuals of *S. miniatus* and *S. levis*. The fishes were apparently following a school of squid, which were regurgitated by the angled fishes and which were caught on lures in the same area. Similarly, in July 1971, a moving aggregation of *S. paucispinis, S. goodei,* and *S. entomelas* was tracked.

DISCUSSION

One probable explanation for the changes in catch rate is that some of the species, notably *S. paucispinis, S. entomelas,* and *S. miniatus,* moved on and off the reef. Alternative explanations, such as periodic reduced feeding rates or reduction of the population due to fishing pressure, are less tenable. No *S. entomelas* were taken during the first 8 months the reef was fished. It is unlikely that the species was present, but not feeding, for 8 months. Increased catch rates, following declines in catches or no catch at all, implies that fishing pressure had not been responsible for the initial decline.

Perhaps deeper-living rockfishes must move relatively more to find sparsely distributed prey. There is some evidence that food for these species is less abundant and more patchy in offshore waters than over shallow reefs (Ahlstrom 1959, 1961; Longhurst 1967; Marlow and Miller 1975). Little is known about how prey patchiness affects the movements of reef fishes, although in general, it has been shown that patchy food resources may lead to greater searching time (MacArthur and Pianka 1966) and larger territory size (Simon 1975, Larson 1977).

Perhaps as the prey of rockfishes is depleted or move out from a reef, some species also leave, either to find new prey sources or to follow the old, as may have been the case on the Twelve Mile Reef. Some deepwater species may be less substrate-oriented than are shallow-water species. *S. paucispinis* and *S. goodei,* for instance, which are abundant over high relief, rocky bottom, are also taken by trawlers over smooth bottom. Certainly, some rockfishes move up into the water column to feed. Lyubimova (1965) noted that *S. alutus* rises 20–50 m during feeding periods. Off the Columbia River, *S. flavidus* fed on myctophids at depths as much as 27 m above the bottom in 137 m of water (Pereyra, Pearcy, and Carvey 1969). During sampling studies I collected *S. paucispinis, S. en-*

tomelas and *S. goodei* as much as 45 m off the bottom, apparently feeding, as they regurgitated fresh prey.

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NOTES

SEASONAL CHANGES IN A POPULATION OF THE FLUFFY SCULPIN, *OLIGOCOTTUS SNYDERI*, FROM TRINIDAD BAY, CALIFORNIA

The fluffy sculpin, *Oligocottus snyderi,* is a common intertidal cottid from northern California to Alaska. North of San Francisco, it lives primarily in the lower intertidal zone. In the mid-intertidal zone, its habitat often overlaps with that of the tidepool sculpin, *O. maculosus,* the abundant cottid of the upper intertidal zone (Nakamura 1976*a*, 1976*b*). South of San Francisco, it is often found in the upper intertidal zone, where the tidepool sculpin is rare (Bolin 1944). Fluffy sculpins tend to be more stenothermal than tidepool sculpins (Nakamura 1976*b*), and associate more closely with specific algae. Despite nearly identical feeding electivity (Nakamura 1971), differences in vertical habitat selection apparently reduce direct competition between the two species (Nakamura 1976*b*). Evidence of resource competition does exist, however, when fluffy sculpins are present with other intertidal cottids (*Clinocottus analis, Artedius lateralis*) along the central California coast; geographic areas where tidepool sculpins are rare (Yoshiyama 1980).

Although age structure and dynamics of tidepool sculpin populations have been previously analyzed along the Pacific coast (Atkinson 1939; Green 1971; Chadwick 1976; Moring 1979), such analyses of fluffy sculpins are lacking. This may be partly due to the absence of scales on fish of this species (for age determination). As a consequence, the collection of large numbers of less accessible specimens is required for size distribution analysis—a more tedious and time consuming method of determining population structure than aging fish using growth rings on scales. Vertebral aging of tidepool sculpins has been used (Chadwick 1976), although resultant age data have not always been comparable to that obtained by other means (Atkinson 1939; Green 1971; Moring 1979). Vertebral aging is extremely time consuming and is impossible for studies where fish are to be returned to the water alive.

The fluffy sculpin closely parallels the tidepool sculpin in its feeding pattern and size range. However, because of distinctive vertical habitat selection by the two species (Nakamura 1976*a*, 1976*b*), different life histories, including age structure, seem likely. To test this, fluffy sculpins were studied in Trinidad Bay, California, from 1967 to 1970, and fish populations were monitored to determine differences in life history characteristics between populations of fluffy and tidepool sculpins.

METHODS

Trinidad Bay, located along the northern California coast about 23 km north of Humboldt Bay, is characterized by rocky shores and scattered tidepools. Between April 1967 and March 1970, 195 fluffy sculpins were collected from lower intertidal pools. Fish were taken each month of the year with a variety of hand nets and seines, anesthetized with quinaldine (Moring 1970), measured (total length), marked with area-specific fin clips (Moring 1976), and released. All fish were released unharmed and alive, with no internal age-determinate structures removed. Length of fish collected ranged from 13 to 101 mm, with a mean of 43.7 mm.

RESULTS

Two dominant age groups, and at least one other age group were distinguishable (Figure 1). The seasonal change in age structure was such that Age I fish dominated the population from winter until mid-summer; then young-of-the-year fish first appeared in collections. The two age groups dominated the population until winter, when growth in length essentially ceased. Yearling fish were absent in the population in November and December (they appeared again in January); though absence in those months may not imply an absence from the population, but rather an absence from collections. The recruitment of young-of-the-year fluffy and tidepool sculpins to the population was indicated by their obvious presence in August collections. I estimated that 56% of the fluffy sculpins examined in August were young-of-the-year and 42% were yearling fish (50% and 46%, respectively, for tidepool sculpins).

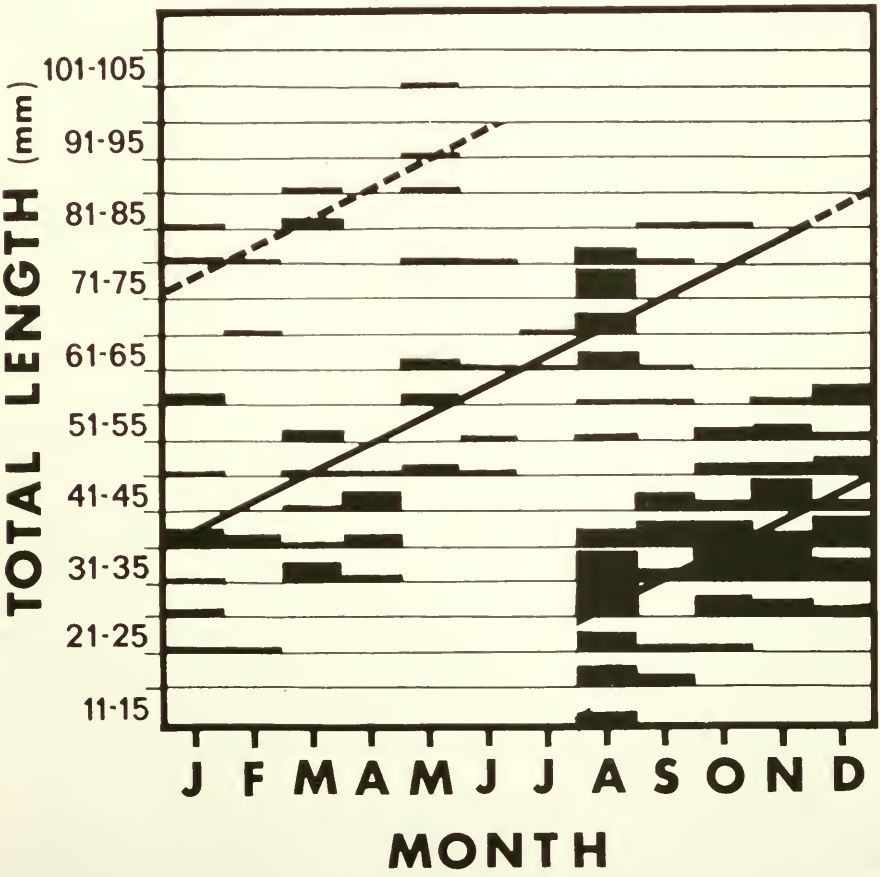

FIGURE 1. Monthly changes in length distribution of fluffy sculpins from Trinidad Bay, California (N = 195). Trends in age groups are visually indicated by the three slanting parallel lines: *bottom,* young-of-the-year (Age 0); *middle,* Age I (the broken portion of the line indicates a presumed growth segment in the absence of collected specimens); *top,* Ages II and older.

Twenty species of intertidal fishes were encountered in Trinidad Bay (Moring 1972). Tidepool sculpins were the most common fish in all areas, but fluffy sculpins consistently ranked second (among year-round residents), accounting for an average of 13% of the total fishes collected. In an examination of three adjoining intertidal areas (see Moring 1976), the percentages of fluffy sculpins in samples were quite consistent: 12, 13, and 15%.

Although population estimates and densities were derived for tidepool sculpins (Moring 1976), too few marked fluffy sculpins were recaptured ($n = 2$; Moring 1976) to estimate population size and densities of that sculpin. Instead, I estimated population density of fluffy sculpins on the basis of the ratio of this species to tidepool sculpins in the sample, and the previously-computed density estimates for tidepool sculpins (Moring 1976). As estimated by this method, there were 1,531 fluffy sculpins in a total intertidal area of 5,025 m^2 (ebb exposed and submerged areas combined), for a density of 0.30/m^2. I believe this figure is reasonably accurate because, when the percent frequency of tidepool sculpins collected in actual sampling is applied to the estimated population derived by Schnabel mark-and-recapture for all intertidal fishes (Moring 1976), the figure is to within 8.2% of the derived population estimate computed just for tidepool sculpins (Moring 1976).

It should be stressed that, although fluffy sculpin density was 0.30/m^2 and tidepool sculpin density was 1.36/m^2 for the total exposed intertidal area, the density of fluffy sculpins will actually be higher within its principal microhabitat (lower to mid-intertidal), and lower in the microhabitat dominated by tidepool sculpins. Because of overlapping habitat selection, it is impossible to estimate the true density of any of the intertidal fish species, except by relating it to the total exposed intertidal area.

DISCUSSION

Two dominant age groups (0 and I) have been indicated in all previous analyses of tidepool sculpins (Atkinson 1939; Green 1971; Chadwick 1976; Moring 1979). Though Chadwick (1976) indicated that as many as six tidepool sculpin age classes may be present (based on vertebral aging), the other three workers positively identified only ages 0, I, II, and possibly III. The present study of a fluffy sculpin population indicates two distinct age groups (0 and I), plus small numbers of older fish. Nakamura (1976*a*, 1976*b*) showed that the fluffy sculpin selects lower level intertidal areas than the tidepool sculpin, and specific habitat requirements tend to restrict the distribution of this sculpin. Hence, fluffy sculpins, are less abundant than tidepool sculpins because they are living in a more restricted habitat in a more rigorous part of the intertidal environment. Yet, I conclude that the population age structure of the fluffy sculpin is similar to the tidepool sculpin in Trinidad Bay.

Cessation of growth during winter months is known to occur in tidepool sculpins (Moring 1979), as well as in certain freshwater Cottidae (Krohn 1968; Petrosky and Waters 1975). A similar retardation of growth can also be seen for fluffy sculpins from the length distribution pattern in Figure 1. Green (1971) showed decrease activity pattern of tidepool sculpins in winter flood tides, as a conditioned response to a season of increased water turbulence; activity is restricted even on days with low turbulence. Since the fluffy sculpin is even less active than the tidepool sculpin (Nakamura 1976*a*), reduced activity would

result in less food being consumed during the principal foraging periods (flood tides) in winter, and hence reduced growth.

Some winter retardation of growth may also be due to conversion of body energy into gonadal development for spring and summer spawning. A lesser metabolic requirement in the presence of lowered water temperature probably plays only a minor role in Trinidad Bay, because Bay water temperatures remain relatively constant year-round (Allen 1964); and tidepool temperatures, though fluctuating widely, averaged 12.6 °C in summer and 12.2 °C in the remainder of the year (Moring 1979). However, even slight changes of water temperature may have a stronger physiological influence on fluffy sculpins than on the more eurythermal tidepool sculpins.

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—John R. Moring, Fisheries Department, School of Natural Resources, Humboldt State University, Arcata, California 95521. Current address: Maine Cooperative Fishery Research Unit, Department of Zoology, University of Maine, Orono, Maine 04469. *Accepted for publication September 1980.*

CONSERVATION OF VERNAL POOL PLANTS IN CALIFORNIA: I. A REPORT ON PIXLEY RESERVE

In a recent book titled "Terrestrial Vegetation of California" (Barbour and Major 1977), numerous contributors commented on California's rich diversity of flora, their somewhat endangered future in many areas, and the need for conservation. Cheatham, Berry, and Hood (1977) summarized the existing "research natural areas" in California, including Federal, State, and other programs. Vernal pools, although seemingly minor in terms of the total area or species number, have drawn increased attention in terms of their island biogeographic structure, high level of endemism, and unique research opportunities in population biology as applied to nature conservation. Current needs in decision-making and the relative inadequacy of research on nature reserve design and management were briefly reviewed by Soulé and Wilcox (1979) and Jain (unpubl. ms). Apparently, too little is known to judge the effectiveness of ongoing programs for protection of species and gene pools. (For a discussion of gene sanctuaries or genetic reserves, as related to crop plants, see Jain 1975.) To quote Cheatham *et al.* (1977) on the justification of research natural areas, "scientists and land managers of the future must be trained to understand nature's complexities. Nature reserves contribute to this need."

This is the first of a series of papers that will attempt to illustrate the place of population biology research in nature conservation. In another paper (Jain, in prep.) we develop some strategies of gene conservation in *Limnanthes,* based on a detailed survey of genetic variation in all of its known taxa. Arguments are developed in terms of the number and relative location of reserves needed for the inclusion of most of the known genetic variation, a research design is proposed to monitor its effectiveness, and long-term demographic and genetic studies are proposed. Similar conservation aspects will be discussed elsewhere for *Orcuttia* (Griggs and Jain, in prep.). In this note we report the species census data spanning a 15-year period for a vernal pool reserve, established by the Nature Conservancy, in order to determine whether a small isolated area (16 hectares) would show extinction of many species. A review of the plant conservation literature showed, however, that even such simple-minded status surveys have rarely been reported (for notable exceptions, however, see Cragg *et al.* 1980, and Soulé and Wilcox (1979)).

McClintock (1976) summarized the chain of events leading to the acquisition by the Nature Conservancy of a 16-hectare site near Pixley, Tulare County, in early 1965. She reported that "a total of 145 species in 102 genera and 36 families were collected" from 1966 to 1969, of which "14 always grow in vernal pools." The species list included grassland species, some California "endemics" like *Chorizanthe uniaristata, Eriognonum gracillimum,* and *Trifolium amplectens;* summer annuals of the genera *Hemizonia, Chenopodium, Amaranthus, Rumex* and *Polygonum,* many Mediterranean weeds, and several species often occurring in but not confined to wet depressions or marshes.

In the spring of 1976, 1979, and 1980, we surveyed several pools for the relative abundance of typical vernal pool species. Data on the presence or absence were summarized in terms of the levels of species diversity per pool (Table 1). The average number of species per pool was significantly higher in 1979; several species (e.g. *Allocarya bracteata, Distichlis spicata, Elatine californica)* were present only in 1979, but estimates of standard errors of species

number per pool showed that different pools shared proportionally more of the same species in 1979 than in 1976 and 1980. Moreover, these estimates of species number per pool are not significantly lower than the overall averages of 10 to 15 species per pool for even larger sets of interconnected vernal pools (Holland and Jain, in press).

TABLE 1. Data on Species Diversity at Pixley Reserve

	Year		
Observations	*1976*	*1979*	*1980*
No. of pools	10	10	7
No. of species/pool*	8.9 ± 2.39	13.1 ± 1.10	10.4 ± 2.44

* Significant among years ($F_{(2,24)} = 11.08$; $P < .01$)

We prepared a list of 31 selected species, with a preliminary survey of their relative abundance in recent years (Table 2). Comparisons of the 1966–69 list by McClintock (1976) and our data show that all except a few species (*Alopecurus Howellii, Callitriche longipedunculata, Tillaea erecta)* in 1966–69 list were seen in one or more recent surveys. In fact, no "extinction" can be ascertained because certain species showed up only occasionally; moreover, in three cases of putative extinctions, the taxonomic identification of taxa in early censuses was open to some question. To estimate the turnover rates one would need perhaps 10 or more years of observations. Other turnover rates, based on short-term data from censuses (Diamond 1969) suggest the need to examine life history features of various groups of organisms. Seed carryover is apparently very crucial in the case of vernal pool species living in temporally variable environments, especially in relation to the patterns of soil water availability. The climatic data on temperature and precipitation for a weather station at Lindsay (near Pixley) showed large variation among the successive years. For example, total monthly preciptation in the winter of 1978 exceeded the 30-year average by more than two standard deviations, whereas seasonal totals for the fall of 1976 and 1978 were below average. Clearly, monthly or weekly patterns of rainfall could be highly correlated with the "periodic appearances" of certain species and there might be certain autocorrelated features of the periodic environment related to the variation in population sizes of different species.

TABLE 2. Summary of Data on Relative Abundance of Selected Plant Species Over a 15-Year Period on the Pixley Reserve.

	Relative abundance in year [1]			
Species	*1966–69*	*1976*	*1979*	*1980*
Allocarya acanthocarpa	*	+	0	++
A. bracteata	*	0	+	0
A. leptoclada	*	0	0	+++
A. undulata	*	++	++	0
Alopecurus specatus	*	++	++	0
Arenaria californica	*	0	0	+
Callitriche marginata	*	++	++	++
Cressa truxellensis valicola	*	+	0	0
Deschampsia danthonoides	*	+++	++	+++
Distichlis spicata	*	0	+	0
Downingia bella	*	++	+++	++
Elatine californica	*	0	++	0
Eryngium vaseyi	*	+	0	+

Hemizonia pungens	*	++	++	0
Juncus bufonius	*	+	0	0
Lasthenia fremontii	*	++	++	+++
Lilaea scilloides	*	++	++	++
Lythrum hyssopifolia	*	+	+	0
Mimulus tricolor	*	+	0	0
Myosurus minimus	*	+	++	+
Orthocarpus erianthus	*	0	+	0
Phalaris lemonii	*	+	++	++
Pilularia americana	*	+	+	+
Plantago bigelovii californica	*	+	0	+
Psilocarphus brevissimus	*	++	+++	0
P. tenuis	*	+	+++	+++
Spergularia marina	*	+	++	+++
Tillaea aquatica	*	+	0	0
Trifolium amplectens		+	0	0
T. tridentatum		+	0	0
Veronica peregrina		+	0	+

[1] present (no notes on relative abundance); 0 absent; + present in fewer than 50% pools; ++ present in 50% or more pools; +++ present in all pools.

We concluded that although no extinctions have apparently occurred in the Pixley pools during the 15-year period, repeated censuses and genetic studies of variation in a few selected species would form the baseline research needed to monitor gene resources. It is somewhat surprising to us that although such opportunities exist in many research natural areas and require rather low-level research funding (albeit long-term), almost no such status reports are readily available. It appears that habitat preservation almost becomes the end rather than the means for conserving biotic diversity after the long, hard-fought weary battles involved in the acquisition of nature reserves and parklands are won.

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—R. F. Holland and S. K. Jain, Department of Agronomy and Range Science, University of California, Davis, CA 95616. *Accepted for publication September 1980.*

DEER USE UNDER BLACK OAKS WITH AND WITHOUT MISTLETOE

Wildlife biologists have long known that common mistletoe, *Phoradendron villosum,* is a favorite food of deer and it is commonly used as bait in trapping deer. Rumen samples from antlerless deer taken from Bartons Flat in November 1952 indicated 2.6% (by volume) of the diet of 38 deer was comprised of mistletoe (unpubl. data). Mistletoe occurred in deer rumen samples from Tejon Ranch (Kern County) from July through April, but occurred most frequently during fall and winter months. It comprised 15% of the total browse diet (browse = 18% of total diet) in January 1968 and 25% of the total browse diet (browse = 33% total diet) during December 1969 (unpublished data). The palatability and digestibility of mistletoe are well documented. Longhurst *et al.* (1968) used cafeteria feeding trials and *in vitro* digestion to measure gas production. They ranked common mistletoe as quite palatable, with a crude protein value of 12%, compared to 16% for alfalfa, *Medicago sativa,* and a relative digestibility of 96%, compared to 100% for alfalfa.

Urness (1969), in studies of mistletoe use by Arizona deer, stated "Mistletoes appear to serve as energy-rich concentrate feeds of particular value to deer during winter". Biswell (1959) measured mistletoe leaf and stem drop from two oaks, one with 24 bunches and another with 9 bunches. Results indicated that 1,821 grams fell during February, March, and April. He found the leaves contained 9.79% protein and 59.79% starch, sugar, and other high energy constituents.

Oak trees that support mistletoe are generally abundant on deer winter ranges. Unfortunately, some land management programs are selectively removing those trees which are heavily parasitized by mistletoe. These treatments have prompted efforts to determine the importance of oaks with mistletoe to deer.

METHODS

This study was conducted on sites within three California migratory deer winter ranges. They included two west slope Sierra sites in Stanislaus and Tuolumne counties and one north interior Coast Range site along the North Fork of the Middle Fork Eel River in Trinity County.

Areas selected for sampling were black oak, *Quercus kelloggii,* types. Vegetation included a mixture of young and old growth yellow pine, *Pinus ponderosa,* and an understory limited primarily to scattered forbs and grasses. An open stand of mountain misery, *Chamaebatia foliolosa,* was found under a few of the oak trees sampled at both the Tuolumne County (Jawbone) and Stanislaus County (Willer Ridge) sites.

Four black oaks, each with 10 or more bunches of mistletoe, and a nearby comparable control tree without mistletoe, were randomly selected at each site. Deer use was determined by deer fecal pellet-group counts on four temporary 10.1m^2 circular plots located four steps from each tree trunk on a north, east, south, and west azimuth. Plots were read during the winters of 1977 and 1978. Thirty or more deer pellets were considered a pellet-group and all groups were recorded regardless of age. The data were analyzed using a standard two-way analysis of variance.

RESULTS

Deer use was significantly higher ($P < 0.01$) under black oaks with mistletoe compared to black oaks without mistletoe (Table 1). Mistletoe was very attractive to deer on all three winter ranges. Depending on the location, trees with 10 or more bunches of mistletoe attracted from 2 to over 12 times more deer use than trees without mistletoe. Although there was a highly significant ($P < 0.01$) difference in deer use between locations, those deer using a particular range demonstrated a very high preference for trees with mistletoe over trees without mistletoe.

DISCUSSION

The high forage value of mistletoe has been verified and its use as preferred forage by wild deer has been reported by many authors (Biswell 1959; Longhurst et al. 1968; Urness 1969). As was expected, deer use under black oaks with mistletoe was greater than under black oaks without. Since most mistletoe becomes available through windthrow and snow breakage (Biswell 1959), one might expect it to be most available at the higher elevations where weather conditions are severe.

In this study, the Trinity County area (Indian Dick) is the highest elevation site at 1,524 m, followed by Willer Basin at 1,371 m, and Jawbone Flat at 1,158 m. The Indian Dick site had the lowest deer use and Jawbone Flat the highest (Table 1). This is inconsistent with the hypothesis that higher elevations and severe weather produce more mistletoe windthrow and increased deer use. Since acorns are an important forage item of deer (Leach and Hiehle 1957; Browning and Lauppe 1964; Short 1975), it appears that the attraction of acorns together with mistletoe might be responsible for the observed difference in deer use between locations and between trees with and without mistletoe.

A good acorn crop occurred throughout most of the black oak range in 1977. No acorns or evidence of an acorn crop were observed in 1978 on the study areas. Fresh acorn caps were plentiful in 1977 under black oaks with and without mistletoe. However, acorn availability data were not recorded. The Jawbone Flat location was the only site sampled in fall 1977. A few fresh acorns were found in the leaf litter while searching for deer pellet-groups. These acorns were cut open and found to be intact. Obviously, this acorn crop attracted deer. A large part of the high deer use (11.4 pellet-groups/10.1 m^2) reported for trees without mistletoe (Table 1) is probably attributable to this mast supply and leaf fall, since virtually none of the live overstory stems or leafage was available to browsing deer and understory herbage and browse were very limited.

No signs of deer bedding were observed under the trees sampled. In 1978, no acorns were observed, yet both the Willer Basin and the Indian Dick locations both supported more deer use under black oaks with mistletoe than without. These observations, together with the deer use data, indicate oaks with mistletoe support more deer than oaks without mistletoe. Another possible explanation for this phenomenon could be that mistletoe parasitism of oaks forces higher acorn production in response to stress factors in infected trees than in non-parasitized trees. This increased acorn production, together with the mistletoe, could attract more deer use. Further investigation is needed to confirm this hypothesis.

TABLE 1. Deer Pellet Groups Under Black Oaks With and Without Mistletoe during 1977–1978.

		Black oaks with 10+ bunches of mistletoe					*Black oaks without mistletoe*				
		Plots					*Plots*				
Location	*Tree*	*1*	*2*	*3*	*4*	*Totals*	*1*	*2*	*3*	*4*	*Totals*
Jawbone Flat	1	32	37	46	35	150(37.5)*	9	7	4	2	22(5.5)
(Elevation	2	45	33	20	23	121(30.3)	20	1	7	2	30(7.5)
1,158 m)	3	13	12	34	18	77(19.3)	23	14	29	15	81(20.3)
	4	12	30	18	20	80(20.0)	11	1	17	21	50(12.5)
TOTALS		102	112	118	96	428	63	23	57	40	183
			Mean/plot = 26.75						*Mean/plot = 11.44*		
Willer Basin.....	1	15	19	16	8	58(14.5)	6	4	14	15	39(9.8)
(Elevation	2	7	4	9	7	27(6.8)	5	4	3	7	19(4.8)
1,371 m)	3	22	17	16	11	66(16.5)	11	3	15	7	36(9.0)
	4	20	23	12	21	76(19.0)	9	5	5	6	25(6.3)
TOTALS		64	63	53	47	227	31	16	37	35	119
			Mean/plot = 14.19						*Mean/plot = 7.44*		
Indian Dick	1	1	13	6	7	27(6.8)	0	0	0	0	0(0)
(Elevation	2	7	3	0	6	16(4.0)	0	0	1	3	4(1)
1,524 m)	3	6	5	6	6	23(5.8)	0	0	0	0	0(0)
	4	4	3	1	2	10(2.5)	0	0	1	1	2(.5)
TOTALS		18	24	13	21	76	0	0	2	4	6
			Mean/plot = 4.75						*Mean/plot = 0.38*		

* ( ) = mean per tree

MANAGEMENT CONCLUSIONS

Mistletoe is an excellent deer forage, particularly on deer winter ranges where forage supplies generally provide low energy diets. Land managers should be cognizant of the wildlife value of mistletoe-infested trees before initiating management programs that might jeopardize this source of high energy forage.

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—Gordon C. Ashcraft, California Department of Fish and Game, 1234 East Shaw Ave., Fresno, CA 93710. *Accepted for publication October 1980.*

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